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SEASONAL POPULATION DYNAMICS OF THE INVERTEBRATE MEROPLANKTON OF SAN JUAN CHANNEL, WASHINGTON, AND STUDIES ON PATTERNS OF LOSS FROM LARVAL POPULATIONS BY PREDATION

by

© JOHN TIMOTHY PENNINGTON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **SEASONAL POPULATION DYNAMICS OF THE INVERTEBRATE MEROPLANKTON OF SAN JUAN CHANNEL, WASHINGTON, AND STUDIES ON PATTERNS OF LOSS FROM LARVAL POPULATIONS BY PREDATION** submitted by **JOHN TIMOTHY PENNINGTON** in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Date 16 June 1986

Abstract

The population dynamics of pelagic larvae of benthic invertebrates of San Juan Channel, Washington, are described, and results of four experimental studies which examine patterns of loss from larval populations by predation are presented. Studies documenting field rates of fertilization of echinoid eggs and depth-regulation by an echinopluteus are included as appendices.

All common and and readily-identifiable types of larvae of benthic invertebrates were enumerated from bimonthly plankton samples taken over two years. Cirripede and lamellibranch larvae were the most abundant larval types, while lecithotrophic larvae were the rarest. Apparent losses from larval stocks were generally 2-3% per day and are ascribed in part to advection and larval depth-regulation. Relatively few larvae occurred in fall and early winter; most larval types could be categorized as either late winter / spring taxa or summer taxa. Late winter / spring species spawned as water temperatures and plankton biomass (phytoplankton) levels were still low but had begun to rise from wintertime minima. Summer spawning species reproduced as temperature and plankton biomass reached maximum levels. Interannual variations in periods of peak larval abundances were correlated with warmer wintertime temperatures during one year. Evolutionary causes and ecological consequences of the above phenomena are discussed.

The experimental studies document laboratory rates of predation by common planktonic predators on a number of species and stages of planktonic embryos and larvae. In the first study embryonic and larval stages of the echinoid Dendraster excentricus were presented as prey to eleven planktivore species. Invertebrate predators were found to eat primarily embryonic or early larval stages while fish preferentially consumed late larvae, indicating that rates of predation are not constant through larval development and that particular patterns of predation may be expected from particular predator taxa. The second study examines the utility of trochophore setae as defenses against planktivores, with the finding that setae deterred predators in all cases. In the third experimental study Garstang's hypothesis regarding the defensive value of torsion for gastropod veligers was tested. The results indicate torsion does not serve as a defense for gastropod larvae. The final predation study documents potential patterns of conspecific and heterospecific predation between medusae and their embryos and larvae in an examination of aggression

between planktonic life-history stages of hydrozoans. No conspecific predation was observed, but heterospecific predaton of adults upon embryos and larvae occurred in the opposite direction to that found between adults of these species.

In a final chapter results of the experimental studies are related so far as is possible to the descriptive chapter; the strengths and weaknesses of all of the studies are evaluated and directions for future research are suggested.

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I am grateful to Dr. Fu-Shiang Chia, who provided unbounded opportunity and who's positive view of progress in science has been a powerful influence in my academic development. I also thank the regular members of my dissertation committee, Drs. A.R. Palmer and A.N. Spencer, for providing good advice during my graduate studies. In addition to the above, Drs. M.G. Hadfield, J.C. Holmes and J.R. Spence served on my thesis examination committee, where they provided valuable criticism.

All of the research described herein was conducted at Friday Harbor Laboratories. I owe debts of gratitude to many of the researchers who conducted work there while I was present. I extend special thanks to Dr. R.R. Strathmann who provided almost daily advice on the innumerable problems I encountered, both specific and general. It may also be appropriate here to acknowledge S.S. Rumrill and R.B. Emlet, who are my my student collaborators on papers included in this thesis.

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I. INTRODUCTION

HISTORY AND JUSTIFICATION OF THE RESEARCH

The basic processes of sexual reproduction are extremely conservative throughout the Metazoa: almost all animals produce gametes which undergo syngamy and then develop through embryonic and often larval stages before a juvenile and thence another adult is produced. Against this conservative backdrop, benthic marine invertebrates exhibit great diversity in sexual reproduction (summarized by Chia, 1974). Eggs can be spawned freely into the seawater to be fertilized, or various forms of copulation can occur. Embryos can develop within or on a parent, or within capsules or envelopes either attached to objects or free in the plankton. The embryos of most invertebrates hatch as larvae which spend variable periods of time (minutes to months) developing in the plankton. Larvae can feed or they may be fueled by yolk; they may resemble adults of the species or not. The termination of the pelagic larval period is marked by a metamorphosis where larval structures are lost and juvenile or adult structures are acquired. All of these variations on a common developmental theme are presumably found in marine invertebrates because of their phyletic diversity, and reflect adaptive interplay between phyletic history and environment (see Strathmann, 1977). Because rates of mortality of planktonic larvae are probably very high (Thorson, 1946, 1950), adaptations which improve larval survivorship should be quickly spread throughout invertebrate populations. This thesis is an attempt to understand how natural selection has molded some aspects of the pelagic larval phases of invertebrate life cycles.

Embryos and larvae of benthic invertebrates became the subjects of embryologists during the 1800's (reviewed by Hyman, 1940). Both before and following the debates surrounding Haekel's formulation of the "Biogenic Law", detailed and now classic morphological descriptions of embryonic and larval types were produced (for fairly recent examples see Mortensen, 1931, 1937, 1938), partially in an effort to construct invertebrate phylogenies. It was not until the late 1800's that the biology of larvae was studied directly, when McIntosh (1889) and Garstang (1893-95) first documented seasonal patterns of larval occurrence in the plankton. Many such "plankton calendars" have since been produced and all are valuable in their respective localities, but

the most extensive study of this sort remains that conducted in Danish waters by Thorson (1946). In that paper and a number of subsequent and wide-ranging reviews (1950, 1953, 1957, 1958, 1961, 1964), Thorson speculated about the fates and functions of planktonic larvae in invertebrate life cycles, formulating what might now be regarded as the dogmas of larval ecology. Thorson's generalizations have persisted largely intact to the present (see Strathmann, 1985, for a recent evaluation), in part because he was extraordinarily insightful, but also because of changing emphases in the study of invertebrate reproductive biology. Though some workers have continued to construct plankton calendars (Chapter II), and others have extensively described invertebrate reproductive (gonadal) cycles (e.g., Giese, 1959; Boolootian, 1966; Giese and Pearse, 1974-79), emphasis in larval ecology per se shifted in the 1950's to experimental analyses of settlement behavior following Wilson's (1948, 1952) finding that polychaete trochophores show substratum selection prior to metamorphosis (see Crisp, 1974, 1985). However, even with experimental science as a powerful influence, the enormity and dilute nature of planktonic habitats has apparently convinced most researchers that ecologically-oriented experiments with truly pelagic larval stages are nearly impossible (Young and Chia, in press). Two notable exceptions, however, are work with larval feeding (e.g., Strathmann, 1971) and study of depth-regulation in some larval types (reviewed in Appendix B). Nevertheless, Crisp (1985) has recently concluded,

> "... our understanding of everything that happens between the release of the egg or larva by the parent and its return to the vicinity of its preferred habitat, is negligible."

This thesis is then an attempt to examine aspects of the planktonic life history of larvae of benthic invertebrates. I have first (Chapter II) constructed a plankton calendar for larvae in the San Juan Channel, Washington State. This chapter is intended to provide a descriptive and comparative base from which more particular questions emerge. The chapters which follow are experimental and are written as a series of papers which address particular questions regarding patterns of predation on planktonic larvae. As described in Chapter II and mentioned above, rates of loss from pelagic larval stocks are

high. However to date, it has proven very difficult to partition the presumed sources of loss; though predation is almost universally thought to be the single largest source of larval mortality (Thorson, 1946, 1950), evidence to support this idea has been entirely anecdotal. The first paper (Chapter III) examines rates of predation by eleven common planktivorous species on echinoid embryos and larvae, and provides evidence that rates of predation upon embryos and larvae are not constant throughout their development, but are stage-specific and often lower on later larval stages. The second paper (Chapter IV) examines the defensive value of motility and the larval setae of trochophore larvae against four planktivorous species, with the finding that setae deter predators in all cases. The third paper (Chapter V) tests the utility of gastropod torsion as a larval defense against seven predator species, with the result that, for the predators examined, torsion does not appear to function defensively. The final paper (Chapter VI) examines patterns of interspecific and intraspecific predation by two hydromedusa species on their embryos and planulae in an examination of levels of control of nematocyst function and the specificity with which predator / prey interactions in the plankton might evolve. Included as appendices are two additional papers, the first of which (Appendix A) documents field rates of fertilization for eggs of a free-spawning invertebrate. Appendix B presents the results of a study to examine both diel and ontogenetic vertical migration of an echinopluteus. All of the experimental sections address problems suggested, implicitly or explicitly, by the descriptive chapter (and see Chapter VII for an evaluation of their success); in addition they center on topics of historic or current interest to invertebrate zoologists.

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II. SEASONAL POPULATION DYNAMICS OF THE INVERTEBRATE MEROPLANKTON OF SAN JUAN CHANNEL, WASHINGTON

INTRODUCTION

The annual cycles of occurrence and abundance of pelagic larvae of benthic invertebrates provide the descriptive basis for the field of larval ecology. Maximum abundances of larvae are limited by the population sizes and fecundities of adult invertebrates, and larval stocks are depleted by mortality and dilution or advection away from suitable benthic habitat. Sources of mortality are predation, lethal physical conditions and starvation (Thorson, 1950), and the numbers of larvae surviving planktonic development to metamorphosis determine rates of recruitment to benthic juvenile and adult populations. In some places or years larval supply greatly exceeds the capacities of benthic habitats to absorb recruits, and in other places or years recruitment fails due to lack of larval supply (Thorson, 1946, 1950, 1966; Connell, 1961, 1975; Oshurkov et al., 1982). In nearly all situations rates of larval mortality are thought to be extraordinarily high, often 90-99% of a population's spawn, but this mortality is offset by the high fecundities common among marine invertebrates (reviewed by Thorson, 1950).

These general conclusions have largely arisen from studies documenting seasonal patterns of larval abundance in the plankton. During the early and middle 1900's such descriptive studies were the primary approach to larval ecology, and a fair number of meroplankton "calendars" have been constructed for various, primarily European, localities (McIntosh, 1889; Garstang, 1893-95; Flattely, 1923; Johnstone et al, 1924; Johnson, 1932; Lebour, 1933, 1947; Battle, 1933; Korringa, 1940; Henderson and Marshall, 1942; Smidt, 1944, 1951; Sulivan, 1948; Jorgensen, 1946; Thorson, 1946; Pyefinch, 1947; Quayle, 1952; Bousfield, 1955; Hannerz, 1956; Grainger, 1959; Carriker, 1961; Shetty et al., 1961; Lonning, 1963; Carli and Sertoiro, 1964; Sentz-Braconnot, 1964; Raymont and Carrie, 1964; Stubbings and Houghton, 1964; Fernaux, 1965; San-Feliu and Munoz, 1965; Vives, 1966; Lie, 1967; Thiriot-Quievreux, 1967, 1968; Bhaud, 1968; Schram, 1968; Seridji, 1968; Mileikovsky, 1970; Cazaux, 1973; DeWolf, 1973; Guerin, 1973; Curtis, 1977; Lough, 1975; LaCalli, 1980; Falk-Petersen, 1982; Oshurkov et al., 1982; Yokouchi, 1984). These studies vary in quality and extent, many concern only

particular larval taxa, and results of all are strongly reflective of local climate, hydrography and fauna. To date only Johnson (1932) has conducted a comparative study of seasonal occurrences of larvae of benthic invertebrates in the northeast Pacific, and his treatment of larvae was necessarily cursory as part of a larger study. Because I believe a more detailed survey of larval occurrences will be of value, I have repeated and considerably enlarged upon Johnson's (1932) work. Both studies were conducted near Friday Harbor, Washington, and the emphasis in both cases is broad and comparative. My purpose has been to describe, in rather broad outline, seasonal patterns of occurrence, maximum abundances, and rates of decline of larval populations at one inland but fully marine site in the northeast Pacific.

STUDY SITE

The study was conducted in San Juan Channel near Friday Harbor Laboratories, Friday Harbor, Washington (Fig. 1; 48° 33' N, 123° W). San Juan Channel runs through a group of islands known as the San Juan Archipelago which separate the Strait of Georgia to the north from the Strait of Juan de Fuca to the south. The channel was produced by glaciation of the British Columbia coastline (Thompson, 1981) and has steep walls and a relatively flat bottom. It runs in a northwest-southeast direction, is about 20 km long, 3 km wide, and 140 m deep.

Tidal exchange between the Straits of Georgia and Juan de Fuca result in strong currents around and through the San Juan Archipelago, commonly reaching speeds of 2.5 m/s in the channels between islands. Most of the exchange passes around the San Juan Archipelago through Rosario and Haro Straits, but about 5% of the tidal flow between the Straits of Georgia and Juan de Fuca passes through San Juan Channel (Thompson, 1981).

Tidal flow around and through the islands largely destroys any vertical stratification of the water column (Thompson, 1981). However, runoff from the Fraser and other rivers produces an estuarine circulation, particularly during summer, characterized by a net seaward flow of surface water (<100 m) from the southern Strait of Georgia out through the Strait of Juan de Fuca. This residual flow typically moves 10-20 cm/s in the middle of the Strait of Juan de Fuca (Thompson, 1981) and presumably flows more quickly through the channels surrounding the San Juan Archipelago. However in spite of this net

southward flow of surface water through the San Juan Archipelago, marine conditions are maintained by advection of coastal water eastward through the Strait of Juan de Fuca. Relatively little water passes south through Johnstone Straits into the northern Strait of Georgia (Thompson, 1981).

Because of scour by tidal currents, the bottom of San Juan Channel consists largely of gravel, cobble and shell debris (Shelford et al., 1935) while the bottom of the Strait of Georgia is mostly silt and clay (Luternauer et al., 1983).

MATERIALS AND METHODS

SAMPLING STATION

Samples were taken at one station near the center of San Juan Channel, 20-200 m northwest of Reid Rock Buoy (Fig. 1). This station was chosen rather than one nearer the laboratory to avoid the low salinity surface layer of water which forms in Friday Harbor during wintertime (pers. obs.), and any local hydrographic effects such as tidal eddys in the harbor. Additionally, Reid Rock rises from the bottom of San Juan Channel (ca. 140 m) to within 3 m of the surface, creating intense local turbulence during tidal exchange. It was felt that the turbulence created by Reid Rock would ensure homogeneous distribution of larvae throughout the water column at the sampling station.

SAMPLING SCHEDULE AND PROCEDURES

Two replicate surface plankton tows were taken weekly during 1983 and 1984, usually during slack tide during daylight hours (standing waves and rapids made boat handling difficult during flood and ebb tide). However on several occasions additional tows were taken in an effort to assess potential sources of variability in the data (Table I): (1) In March, 1983, six replicate surface tows were taken, and in April, 1983, two replicate surface tows were taken during each of ebb and low slack, and one tow was taken during flood tide; (2) on three dates during 1984 two replicate vertical hauls (0-80 m) were taken in addition to the normal weekly surface tows for those dates. In sum almost 250 plankton tows were taken over 2 years.

All samples were taken with the same plankton net equipped with 125 um nylon mesh. The net was 1.4 m long, conical, and its mouth was held open by a 25 cm diameter steel ring. A TSK (Tsurumi-Seiki-Kosakusho Co.) flowmeter was mounted off-center in the mouth of the net and served both as a weight and to measure volume of water sampled. The volume of water filtered per revolution of the flowmeter impeller was assessed by towing the steel ring and flowmeter, both with and without the netting attached, known distances between two docks in Friday Harbor.

Surface tows were taken by towing the net 1-2 m deep about 15 m behind a skiff at idle speed (ca. 1 m/s). During winter the net was towed for 10 min, but because of clogging by phytoplankton, tows had to be reduced to 5 or 2.5 min during spring and summer. Vertical hauls were taken by hand, or occasionally with an electric winch, both of which retrieved the net at about 0.5 m/s. Upon retrieval of the net, the plankton was washed into jars to make samples of about 500 ml; 25 ml of 2.5% propylene phenoxetol was then added as an anaesthetic (McKay and Hartzband, 1972). Temperature and salinity of surface water were measured (Yellow Springs Instruments conductivity meter, and later an American Optics temperature-compensated refractometer; the YSI meter became unreliable in the latter part of 1983 and gave low readings in a non-systematic way), and general notes were taken regarding tidal conditions and weather. Samples were then returned to the laboratory and fixed in 10% formalin (sodium borate-buffered) after about 30 min in anaesthetic.

SAMPLE ANALYSIS

Many more plankton samples were collected than were intended for analysis because of the relative ease of collection and storage of samples for any possible future use. Thus, only samples from biweekly intervals were examined (Table I). In addition, because sorting of the samples (see below) proved very time-consuming, only 1 of the 2 replicate samples for each date was usually sorted (Table I).

Plankton samples were stored in formalin 1-14 months prior to sorting. Preparatory to sorting, samples were subsampled with a Folsom plankton splitter (McEwen et al., 1954) so that during winter, 1/4 or 1/8 of an entire sample was sorted, but during spring and summer when larval (and phytoplankton) abundances were high, only

1/16 to 1/64th of a sample was generally sorted (Table I). If less than 100 of the most abundant larval type were found in a subsample, another equal subsample was sorted. The wet weight of the unsorted portion of a sample was obtained after fluid was drained off through 41 um Nitex mesh for 5-15 min. After weighing samples were resuspended in filtered seawater and formalin. The splitting procedure and the necessary practice of towing the net for shorter periods during spring and summer probably resulted in under-representation of rare larvae during these periods (see also Rees, 1954a, 1954b, for a similar problem). In part for this reason, emphasis throughout has been placed on the occurrence of common larval types.

Thin layers (1-2 mm deep) of the subsamples were carefully examined in Bogorov trays under a dissecting microscope at 25X. Masses of phytoplankton and zooplankton were teased apart with needles, and it was found that addition of a drop of detergent flattened the surface meniscus so that all areas of the tray could be viewed clearly. The first 100 individuals of each readily-identifiable larval type (Table II) was individually pipetted into 5 ml vials for reference and possible detailed examination at a later date. Larval types were usually identified with the aid of general references such as the "Fiches d'Identification du Zooplancton" (1957-83), Newell and Newell (1963) and Smith (1977), but additional references were used during the identification of some specific larvae (see Results). All larvae of each type within the subsamples were counted with a "blood cell calculator" (a multiple-register hand tally; Marbel Co.) and records of the counts, rough sketches of many of the larvae, and general notes were compiled. It was found that 6-12 actual sorting hours were required to enumerate larvae within the subsample(s) representing each tow.

The numbers of larvae of particular types observed per subsample were standardized to number of individuals per cubic meter of plankton by dividing direct counts of larvae by the portion of a sample actually sorted, and dividing these figures by the volume of water sampled during that tow as estimated by the flowmeter. As a consequence of this standardization many more larvae in wintertime samples (when the duration of plankton tows was long and a larger split of each tow was generally sorted) were required to produce a given number of larvae per cubic meter than in summertime samples (when tows were short and a smaller splits were sorted). The conversion factors

responsible for this artifact are listed in Table I; these figures represent the estimated number of individuals per cubic meter for each larva directly observed in the subsamples. This characteristic could produce misleading results during statistical analysis of the standardized data. In part for this reason all statistical tests used were nonparametric (see Sokal and Rohlf, 1969). Statistical analyses were conducted by correlating biweekly measurements between years (1983 and 1984) using Kendall's Coefficient of Rank Correlation (KCRC). This statistic provided a measure of association or correlation (tau) between variables analogous to the correlation coefficient of regression analysis, and also tested whether or not the observed patterns of larval abundance were significantly correlated (similar) between years (Sokal and Rohlf, 1969). The Wilcoxon Signed Rank Test (WSRT), a nonparametric analogue of the paired-sample t-test, was also used to determine if differences in mean larval abundances were statistically significant between years. Because samples were not taken on exactly the same date each year (Table I), these paired-sample statistics were calculated with mean bimonthly larval abundances.

RESULTS

ENVIRONMENTAL CORRELATES

Temperature

Surface seawater temperature did not undergo great seasonal fluctuations in San Juan Channel. During both 1983 and 1984 seawater temperature varied about 6° C, with a minimum temperature of 6.5° occurring in December or January and maximum temperatures of about 13° occurring during late summer (Fig. 2). Additionally, the general pattern of temperature change, with slowly increasing temperature between January and August and a relatively rapid decrease in temperature after September, was similar both years and resulted in a significant correlation of temperatures cycles between years (KCRC, tau=0.9, $P<0.001$). However, the mean surface temperature during 1983 was 0.7° warmer than during 1984, primarily due to warmer wintertime temperatures (ca. 2°) in 1983. This difference is statistically significant (WSRT, $P<0.001$).

Salinity

Surface salinities did not vary greatly and showed no clear seasonal patterns except for some reductions during spring and summer which were probably due to increased flow of the Fraser River resulting from snowmelt (Fig. 3). This spring-summer depression does not result in significant correlations in bimonthly salinities between years (KCRC, tau=0.0, P=0.4). Mean salinity was significantly lower during 1983 (25.9 ppt) than during 1984 (27.5 ppt) (WSRT, P=0.046), but as noted previously, the first salinometer became unreliable and generally gave low readings during late 1983 before it was replaced. Because general trends were not strong or clearly cyclical, salinity changes are largely disregarded in the following discussion.

Plankton biomass

Drained wet weight of the plankton samples was measured to provide an index of general plankton biomass. During winter and early spring, samples were small and consisted largely of zooplankton. From May through September, however, plankton biomass underwent striking increases and consisted mostly of phytoplankton. Biomass cycles for both years were similar (Fig. 4) and highly correlated (KCRC, tau=0.5, P<0.001) with the exception of two low values during summer of 1984. Wet weights were significantly higher during 1983 (0.7 g/m^3) than in 1984 (0.6 g/m^3) (WSRT, P=0.046), in part because of the 2 summertime low values in 1984, but also because springtime increases in plankton biomass began about a month earlier in 1983. These trends in plankton wet weight are taken as indicative of general seasonal cycles in phytoplankton abundance with some minor contribution by zooplankton biomass. Unfortunately, most of the phytoplankton retained by the net consisted of large cells that are probably not fed upon by most larval types (Thorson, 1946, 1950). It is not known to what extent the seasonal dynamics of smaller algal species (more likely to be eaten by larvae) may differ from the observed trends, though there is some indication that small flagellates may be proportionally more abundant than diatoms during winter (reviewed by Harrison et al., 1983).

LARVAL OCCURRENCE

The benthic invertebrate fauna of the San Juan Archipelago is diverse (see Kozloff, 1974) and partly as a consequence most of the local meroplankton cannot be identified below phylum or class level. Many published descriptions of larval development are not useful to a study of this kind (see Chanley and Andrews, 1971) either because (1) little comparative information is given within the taxon of interest, or (2) because of the labor involved in identification (for example, examination of lamellibranch veliger hinges; Rees, 1950). In addition (see Discussion), most of the larvae observed were relatively young stages, prior to the formation of many features that might be used in species identification. As a result most of the larvae examined in this study were incompletely identified. Under each of the following headings, however, I have included a brief discussion of which invertebrate species were likely to have produced large fractions of the larvae observed.

The following groups of larvae were found in the plankton in fairly large numbers. Larvae not included in the types discussed below were not found in the plankton samples at all, or with such low frequency that their occurrence was considered incidental (e.g., <>10 larvae observed throughout). For a discussion of the reliability of the following estimates, see "Sources of Variability".

Polychaeta

Kozloff (1974) provides keys to over 200 species representing 40 families of common polychaetes fom Puget Sound and the San Juan Archipelago. Many if not most of these species produce pelagic larvae for which descriptions are lacking. Identifications of some common, late trochophore larvae might have been attempted, but because it was not feasible to routinely examine live larvae (as did Thorson, 1946; LaCalli, 1980) such identifications would have been based on examination of the setal types of each trochophore (e.g., Blake, 1975a, 1975b). An alternate approach might be to identify numerically dominant and fecund local species which produce pelagic larvae, and to infer their contribution to larval populations. Although this approach appears to have some utility for other taxa (see below), one or a few polychaete species have not been described as dominant community members during local faunistic surveys (see Shelford

and Towler, 1925; Shelford et al., 1935). The results presented below thus represent abundances of all trochophore larvae encountered; it is also possible that a very few non-polychaete (e.g., sipunculan, etc.) trochophores were also included under this heading.

Polychaete trochophores occurred in the plankton from February through October of 1983 and September of 1984 (Fig. 5). The broad patterns of abundance were significantly correlated between years (KCRC, tau=0.05, P<0.001). Mean trochophore abundance was substantially lower in 1983 (70.9 ind. / m^3) than in 1984 (95 ind. / m^3), though the WSRT indicated these differences in between-year abundances were not quite significant (P=0.053). The curve for each year shows five peaks in trochophore abundance which are fairly synchronous between years but vary considerably in magnitude. It is not clear which or how many of these peaks represent larval cohorts of the same or different species.

Mollusca: Gastropoda

As with the Polychaeta, gastropod diversity in the San Juan Archipelago is high (see Kozloff, 1974) and veligers of few local species have been described. Shelford et al. (1935) described 5 gastropod species as dominant members (2-150 ind. / 10 m^2 each) of the benthic community characteristic of San Juan Channel habitats. The broad patterns of larval abundance described below probably indicate substantial contribution by several relatively abundant gastropod species.

The between-year occurrence of gastropod veligers was highly variable (Fig. 6) and the patterns of seasonal occurrence were not significantly correlated (KCRC, tau=0.2, P=0.15). This non-correlation resulted from the high relative variation in veliger abundance during 1984, or its lack in 1983. Absolute mean veliger abundances were also much lower in 1984 (20.9 ind. / m^3) than in 1983 (50.2 ind. / m^3)(WSRT, P<0.001). The absolute values of the variations in veliger abundance during 1984 were not high; it is not clear to what extent this is random variation around a low mean abundance of larvae during 1984.

Mollusca: Lamellibranchia

Although Kozloff (1974) lists 120 local bivalve species, only a few of these are abundant enough to have contributed large proportions of the veligers observed in the plankton samples. Most notably, Shelford et al. (1935) found Modiolus rectus [as M. modiolus] in beds of 10-3000 individuals per 10 m^2 and Chlamys spp. [as Pecten hericius] in densities of 15-1000 ind. / 10 m^2 throughout San Juan Channel. Because these species are so common, most of the lamellibranch veligers observed were probably M. rectus or Chlamys spp. though a number of other bivalve species were undoubtably also present.

Lamellibranch veligers were very abundant during the summers of both 1983 and 1984, reaching peak abundances of over 800 ind. / m^3 (Fig. 7). Even this figure is almost certainly an underestimate because early veligers of many species are small and would not have been sampled by the net (125 um mesh). The between-year patterns of abundance were significantly correlated (KCRC, tau=0.4, P=0.006), though as with the gastropod veligers, there was considerable variation in pattern of abundance. Also similar to the gastropod data, mean bivalve veliger abundances were significantly higher in 1983 (239 ind. / m^3) than in 1984 (111 ind. / m^3) (WSRT, P<0.001) though the peak abundance was actually higher in 1984 (in contrast to the gastropod veligers). The two major peaks in veliger abundance during 1984 are synchronously matched by the largest peaks of 1983.

Crustacea: Cirripedia

Only about 7 species of barnacle are common in the San Juan Archipelago (see Kozloff, 1974), and several of these are very common in San Juan Channel and were certainly present in the plankton samples. Some species could probably have been identified on the basis of naupliar setation (see Brown and Roughgarden, 1985), but this was not attempted.

Cirripede nauplii were the most abundant larval type observed over the course of this study (Fig. 8) and almost certainly outnumbered all other zooplankters during their peak occurrences. Mean abundance was 312 ind. / m^3 during 1983 and 369 ind. / m^3 during 1984, with a peak abundance of 2580 ind. / m^3 during May, 1983. Seasonal patterns of abundance were highly correlated between years (KCRC, tau=0.7, P<0.001) and three peaks of abundance appeared on the same dates each year. Mean abundances between

years were not significantly different (WSRT, P=0.36), though in contrast to the gastropod and lamellibranch data, cirripede nauplius mean abundance was higher during 1984.

In spite of the large numbers of cirripede nauplii found during spring and summer, cirripede cypris larvae were rare both years (Fig. 9). Mean abundances were so low (1983, 1.0 ind./m^3; 1984, 0.2 ind./m^3) and variable that these data indicate little other than periods of cyprid presence. Nonetheless, cyprids were present during March and April of both years, during and possibly following the earliest peak of nauplius abundance (Fig. 9). Curiously, cyprids were not present either year following the May-June nauplius peak occurrence but were present both years in late summer and fall after the last (July) peak in nauplius abundance. Cyprid abundances were roughly three orders of magnitude less than those of cirripede nauplii.

Crustacea: Brachyura

Kozloff (1974) provided keys to adults of 27 local brachyuran decapod species, and Hart (1971) constructed a key to the larvae of 6 brachyuran families found in British Columbia waters. Large swarms of brachyuran zoeae occur during spring off the floating breakwater at Friday Harbor Laboratories. In spring of 1983 Rumrill et al. (1985) found most of these to be cancrid zoeae, and most of the brachyuran zoeae observed in the present study were probably Cancer spp. Megalops larvae were never found in the samples.

Occurrence of brachyuran zoeae was limited to spring and early summer of both 1983 and 1984 (Fig. 10). The seasonal patterns of occurrence were highly correlated between years (KCRC, tau= 1.0, P<0.001) but peak abundances were significantly higher in 1983 (6.2 ind./m^3) than in 1984 (5.3 ind./m^3)(WSRT, P<0.001). The curves for both years show a single peak of zoea abundance during late March and April.

Bryozoa

Almost all the cyphonautes larvae observed were presumably Membranipora membranacea (see Atkins, 1955a, 1955b; Ryland and Hayward, 1977), though it is conceivable that another, similar cyphonautes was also present (C. Reed, pers. comm.). A

very few, distinctive cyphonautes were found which were probably Conopeum reticulum (see Cook, 1964; Cook and Hayward, 1966), an estuarine species which occurs in Puget Sound (Kozloff, 1974).

During both 1983 and 1984, cyphonautes larvae occurred primarily in late summer (Fig. 11). The seasonal patterns of occurrence were significantly correlated between years (KCRC, tau=0.3, P=0.018) and there were no significant differences between mean annual larval abundances (1983, 10.8 ind./m^3; 1984, 10.3 ind./m^3) (WSRT, P=0.14). The curves for both years are remarkably similar. In late March and early April low numbers of cyphonautes began to occur and these abundances persisted until early July when large numbers of larvae were found. The July peak declined through August and September but was followed by a second, smaller peak in October.

Echinodermata: Echinoidea

Although 7 echinoid species occur in water surrounding the San Juan Archipelago, only 2 are abundant in San Juan Channel. Strathmann (1977) has constructed a key to the larvae of local echinoids. Plutei observed in the plankton samples were almost all Strongylocentrotus droebachiensis or S. franciscanus. Some plutei of Dendraster excentricus were, however, encountered. Plutei were staged by number of arms, but these data have not been presented because over 95% of the plutei (excepting D. excentricus) observed were early, 4-armed larvae. Temporal trends were not apparent in the data for the few older larvae observed.

Echinoplutei occurred in the plankton from March through August of 1984 and October of 1983 (Fig. 12). These seasonal patterns of occurrence are significantly correlated (KCRC, tau=0.7, P<0.001). Mean number of plutei in 1983 (4.1 ind./m^3) was also significantly lower than mean abundance in 1984 (6.9 ind./m^3)(WSRT, P<0.007). During both years a March peak consisting of about equal numbers of both S. droebachiensis and S. franciscanus plutei was followed in late April (1983) or in May (1984) by a second, major spawning of S. franciscanus. Larvae occurring after June were primarily 6 or 8-armed D. excentricus plutei which occurred in low numbers throughout summer of both years and fall of 1983.

Echinodermata: Ophiuroidea

Accoring to Kozloff (1974), 12 species of ophiuroids are common in Puget Sound and the San Juan Archipelago; 10 of these produce planktotrophic larvae (S. Rumrill, pers. comm.) that might have been encountered in the plankton samples.

Although never found in large numbers, ophioplutei occurrred in two peaks of abundance from February through March and from June through October in both years (Fig. 13). These seasonal patterns were significantly correlated between years (KCRC, tau=0.3, P=0.02), but mean abundance in 1983 (2.6 ind. / m^3) was significantly less than in 1984 (4.8 ind. / m^3)(WSRT, P<0.01). Because the winter / early spring and the late summer peaks in larval abundance occurred both years they probably represent larval production by at least two species.

Echinodermata: Holothuroidea and Asteroidea

At least 13 holothurian and 18 asteroid species occur in the San Juan Archipelago (Kozloff, 1974), and 10 of these produce feeding larvae while most of the remainder produce large, yolky eggs and larvae (M. Strathmann and S. Rumrill, pers. comm.). Beyond this distinction between feeding and non-feeding larvae, however, holothurian and asteroid larvae were not separated. Most planktotrophic larvae observed were early holothurian auricularias, prior to formation of the posterior larval ossicle, or early asteroid bipinnarias (which do not develop larval ossicles). It was thus not possible to separate the larvae on the basis of ossicle development. Additionally, in fixed early larvae it was difficult to determine if the ciliated band had broken into two loops as is characteristic of asteroid bipinnarias. Lecithotrophic holothurian and asteroid larvae were also not separable on the basis of obvious external morphology, though these larvae did retain their original colors in formalin. Measurements of larval size were also of little use with fixed specimens, because unknown amounts of shrinkage probably occurred during fixation and storage. For these reasons holothurian and asteroid larvae could not be separated on morphological grounds. However, the relative abundance of adults of these species probably indicates which species produced most of the larvae found in the plankton. While all of the asteroid species are relatively rare (<2 ind. / 10 m^2; Shelford et al., 1935), both Parastichopus californicus and Cucumaria miniata are found in high densities in San Juan Channel (2-30

ind./ 10 m²; Shelford et al., 1935), and both species produce large numbers of eggs (McEuen, 1986). However, P. californicus produces planktotrophic auricularias while C. miniata spawns large yolky eggs that become lecithotrophic larvae. Most of the larvae discussed below were probably of these species, while asteroid larvae were not well-represented in the samples.

Planktotrophic holothurian or asteroid larvae occurred in relatively low numbers in the plankton from late March through October of both 1983 and 1984 (Fig. 14), with a first minor peak in abundance in late March to early April, and a large increase in abundance in late May (1983) or early June (1984). These patterns of occurrence are significantly correlated between years (KCRC, tau=0.5, P=0.002), but mean larval abundance was significantly less in 1983 (3.0 ind./ m³) than in 1984 (6.9 ind./ m³)(WSRT, P=0.04). One or two additional peaks in abundance occurred in July or August.

Lecithotrophic holothurian and asteroid larvae were never abundant in the plankton samples, in part because eggs and larvae of many species are buoyant and are often observed floating on the surface (Johnson, 1932) even in highly turbulent areas. The plankton net towed 1-2 m deep thus did not sample larvae floating at the surface. Nonetheless during both 1983 and 1984, peak abundances of lecithotrophic echinoderm larvae occurred in early April (Fig. 15). In 1983 these larvae were also found in low numbers in February, April and August, but in 1984 yolky holothurian or asteroid larvae were also found in early June. These seasonal patterns were significantly correlated (KCRC, tau=2.3, P<0.001). The WSRT indicated mean abundance was also significantly higher in 1983 (1.9 ind./ m³) than in 1984 (1.3 ind./ m³) (P<0.001), primarily because larvae occurred on 6 dates in 1983 but only 3 dates during 1984. The April peak abundance probably represents a single larval cohort; the earlier and later peaks presumably reflect additional spawnings by the same or other species that occurred or were sampled only during one of the two years. Almost all of the yolky larvae observed were pale green in color.

Urochordata

As with lecithotrophic holothurian and asteroid larvae, ascidian tadpole larvae were never abundant in the plankton samples (Fig. 16). Tadpoles occurred sporadically

throughout both years, excepting a 3-4 month absence during summer of 1984. These patterns of larval occurrence are significantly correlated between years (KCRC, tau=0.5, P=0.002). The WSRT indicated mean abundance of tadpoles was significantly higher during 1983 (1.0 ind./m³) than in 1984 (0.8 ind./m³) ($P<0.04$), primarily because tadpoles were found on twice as many dates in 1983. These results indicate that ascidians in San Juan Channel spawn or release larvae throughout the year, although summertime breeding may be uncommon some years.

SOURCES OF VARIATION

Most of the seasonal patterns of larval abundance presented above are highly correlated between years, indicating (1) that larvae within particular taxa were present at about the same time and in similar (though often not equal) abundances both years, and (2) that the plankton samples provided repeatable measures of these patterns for the more abundant larval types. However, apart from these observations it has not been determined how such factors as stage of tide or time of day during which the samples were taken might have contributed variability to the data. Several attempts were made to address these questions, though these were limited by the amount of plankton that could be sorted. The results indicate that a number of factors contribute substantial variance to the observed numbers of larvae.

Horizontal patchiness

Small scale horizontal patchiness (on the order of 300 m, the approximate length of the surface plankton tows) was estimated by sorting replicate samples taken sequentially (see Methods) on each of 9 dates (Table I). The mean coefficient of variation (CV) between these replicates for all taxa with >10 ind./m³ was 27%, indicating that samples taken at the same location only minutes apart could contain quite variable numbers of larvae. The numbers of the various larval types caught in 6 replicate tows taken sequentially on 3/14/83 (Table I) are presented in Figure 17. As discussed above, numbers of larvae sampled were quite variable between tows, and there is some indication of non-independence of counts between the larval types. For example in Tow #2, polychaete, lamellibranch and cirripede larvae were all more abundant than in the other

tows. However when analyzed by Friedman's analogue for 2-way analysis of variance, the variations in numbers of larvae sampled between the tows are non-significant ($P>0.5$). Similarly, when numbers of larvae captured between 10 sets of additional replicate tows (Table I; but not 1/17/84 when few larvae were present) are compared by the WSRT, in only 2 of the 10 cases are paired differences in number of larvae caught between tows significant ($P<0.05$). If significant differences in numbers of the various larval types had routinely occurred between replicate tows, the most likely explanation would have been that the measurements of volume of water filtered were innacurate.

Samples were not taken at different stations in San Juan Channel or elsewhere to examine horizontal patchiness on a broader scale, but on one date in 1983 (Table I), 2 replicate tows were taken during each of ebb and low slack tide, and one tow was taken during flood tide. Tidal current probably separated each set of samples of this series by at least several thousand meters of water, and the tows were also separated by several hours' time (ca. 3 hr intervals between samplings). Again, variations in larval abundance were substantial between tows taken at different tidal stages (Fig. 18), with an overall mean CV of 45%. Cirripede nauplii were most abundant during slack tide, but most other larval types were more abundant during ebb or flood tide. It is probable that these changes reflect interactions between larval depth-regulation and turbulence created by tidal currents (see below).

Vertical distribution

It was also of interest to determine if the turbulence at Reid Rock Buoy actually produced homogeneous vertical distributions of larvae. On 3 dates during 1984 (1 each in winter, spring and summer), 2 replicate vertical hauls (0-80 m) were taken in addition to the routine horizontal tows for those dates (Table I). When standardized to number of larvae per cubic meter, most larval taxa were found to be more abundant in the vertical hauls (Figs. 19-21). Cirripede nauplii, however, were more abundant at the surface than at depth on the springtime date they were abundant (Fig. 20). If cirripede nauplii swam upwards while the other larval types avoided the surface, the patterns of abundance observed in the samples during the tidal series (Fig. 18) may reflect the ability of larvae to regulate depth (see Appendix B) during slack but not during ebb or flood tide when currents are

strong. That larvae might be vertically stratified at this site was quite surprising (see DeWolf, 1973, 1974); the routine surface tows apparently did not sample the depths of maximum abundance of a variety of larval types. Because most larval types apparently avoided the surface at least during slack tide, it would have been of some interest to compare vertical distributions of larvae between night and daytime.

DISCUSSION

REPRODUCTIVE SEASONS

General patterns

As is widely recognized, most middle and high-latitude invertebrate species reproduce during periods of rising water temperature and phytoplankton production or biomass (Thorson, 1950). This pattern was apparent for most of the larval types in the present study (Table II). However, several authors have noted that species with lecithotrophic larvae or directly developing young which are not dependent on phytoplankton for food reproduce in fall or winter or at least have prolonged spawning periods (Thorson, 1946, 1950; Giese, 1959; Curtis, 1977; LaCalli, 1981; Falk-Petersen, 1982). In the present study ascidian tadpole larvae were present year-round, but so few tadpoles were encountered it is not clear if this pattern is more apparent than real. The only other lecithotrophic larvae to occur repeatedly in the samples were holothurian or asteroid species; these were present in springtime at about the same time as the first peaks of planktotrophic echinoderm larvae. Falk-Petersen (1982) has suggested that larvae produced during wintertime experience less competition for settling space and other benthic resources as juveniles, and Curtis (1977) suggested that wintertime reproduction enables the resulting juveniles to take full advantage of the subsequent spring/summer periods of primary production. Both of these ideas are probably to some extent correct, but my observations of springtime occurrence of lecithotrophic larvae would apparently indicate that springtime reproduction can be advantageous even for non-feeding larvae. Perhaps an optimal solution for species producing lecithotrophic larvae (and also direct developers) would be to reproduce immediately prior to spring phytoplankton blooms and

temperature increases, thus avoiding the springtime population increases of a variety of planktonic predators (e.g. hydromedusae; Milis, 1981) and also any competition for benthic resources as larvae settle. The resulting juveniles should then be able to exploit springtime production and begin to grow almost immediately. Although little is known of size-related or seasonal mortality schedules for juvenile invertebrates, the smallest size-classes probably experience the highest rates of mortality (see Thorson, 1966), and high juvenile growth rates should be advantageous. While this scenario of seasonal reproduction may indeed be optimal, a number of larval types were nevertheless abundant in late summer or fall.

Almost all planktotrophic larvae were found during late winter, spring, or in summer (Table II). If occurrences of the larval types are compiled by season of peak abundance (Fig. 22), it becomes apparent that most larval types characteristically occurred either during late winter to spring, or in summer. Thus polychaete, gastropod, lamellibranch and bryozoan larvae were most abundant during summer, while echinoderm and crustacean larvae were most abundant in late winter and spring. The late winter / spring larvae, whether planktotrophic or lecithotrophic, were spawned while temperatures and "plankton biomass" were still near low wintertime levels but had just begun to increase (Figs. 2, 4, 22). So far as plankton biomass can be taken as an estimate of food abundance (see Environmental Correlates, above), it might be assumed that these larvae encounter relatively poor feeding conditions. The combination of low temperature and low food abundance might result in relatively slow rates of larval development. As pointed out by Thorson (1946, 1950) and Korringa (1957), any slowing of development could result in higher overall mortalities, primarily due to increased periods of exposure to planktonic predators (see Chapters III-VI). However as noted above, it may be that abundances of predators in late winter or early spring are relatively low, and that due to low temperatures feeding rates of predators are also low during these months. Additionally, larvae metamorphosing after several weeks (see Thorson, 1946) of late winter or springtime development should experience conditions generally favorable to rapid growth through summer as discussed above.

Larvae of summer spawning species encountered near maximum water temperature and plankton biomass (Figs. 2, 4, 22), and both feeding and temperature

conditions should have fostered rapid development to metamorphosis. However, these larvae are present in the plankton during a period when predators are also abundant, and juveniles resulting from late summer or fall metamorphosis will presumably have to persist through winter at small and vulnerable sizes.

The cycle of abundance of cyphonautes larvae is perplexing because it does not conform to the above patterns. Cyphonautes larvae first appeared in the samples in March and April and then exhibited two peaks of abundance, the first in summer and the second in fall. Except for a very few larvae which were identified as Conopeum reticulum (Cook, 1964; Cook and Hayward, 1966), all of the larvae encountered in the samples agreed with descriptions of Membranipora membranacea (Atkins, 1955; Ryland and Hayward, 1977), and it is considered unlikely that the summer and fall peaks of cyphonautes abundance represent production by two species. Because few or no adult M. membranacea survive winter in the San Juan Archipelago (Harvell, 1985), cyphonautes larvae appearing in March and April must represent the founders of the summertime population. These springtime larvae may originate from local colonies which overwinter, or that they may be advected from the outer coast where adult populations persist year-round (S. Rumrill, pers. comm.). These springtime larvae presumably metamorphose and develop into reproductive colonies which produced the major summertime peak of cyphonautes. However, the summertime cyphonautes are apparently unable to settle and reproduce locally (Harvell, 1985). Additionally, Harvell (1985) found that most adult colonies were dead or dying by September. Even though larval production is cued by deteriorating conditions for adult growth, it is not clear where the fall larvae originated. Yoshioka (1982) found patterns of cyphonautes abundance in sourthern California surface waters which were negatively correlated with thermal stratification of the water column; cyphonautes apparently avoided warm (>15°) surface waters. Although surface temperatures were less than 15° throughout the present study, cyphonautes larvae were more abundant at depth on one date in early September than at the surface (Fig. 21). Although cyphonautes were abundant at the surface earlier in summer when tempratures were also high (12-13°), it is possible that larval depth-regulation affected the patterns observed. In any case the cyphonautes larvae found in October and November almost certainly do not overwinter locally as larvae; they are probably advected into the Strait of Juan de Fuca and lost to local populations

(see Larval Abundances, below).

The above interpretations of the seasonal patterns of larval abundance presume that because the observed taxa occurred in the plankton (and were often abundant), the seasonal patterns of abundance represent successful or even optimal solutions to the problem of reproduction in the San Juan Archipelago. Such assumptions are only partially justifiable. Species with dispersing larvae often occur over wide geographic ranges (Thorson, 1961; Mileikovsky, 1962; Scheltema, 1971), and it is usually not possible to determine to which portion of its range a species is "optimally" adapted. For example in the present study, it is not possible to decide whether the two patterns of late winter / spring or summer reproduction are locally adaptive, or whether the patterns are marginally successful and are functions of temperature or other cycles representative of the biogeographic ranges of the species involved. This ambiguity might be resolved with sufficient information concerning both larval and juvenile population demographics, but it is likely that at least some of the observed patterns are not locally adaptive. As a possible example, Strongylocentrotus droebachiensis plutei are abundant in surface waters off the west coast of Vancouver Island during winter (S.S. Rumrill, pers. comm.). Although adult S. droebachiensis are abundant in San Juan Channel, their plutei were found only in low numbers during March in the present study (see also Larval Abundance, below). Similarly, the fall peak of cyphonautes abundance probably does not result in recruitment, at least locally.

A number of authors have correlated peak periods of larval abundance with the biogeographic ranges of the species involved (Sullivan, 1948; Bousfield, 1955; Bhaud, 1967; Mileikovsky, 1970; Falk-Petersen, 1982) and concluded that at a given site characteristically higher latitude species reproduce earlier than do lower latitude species. Additionally as one moves away from the equator, spawning periods of both species and communities become compressed, coinciding with the shorter periods of primary production in higher latitudes (reviewed by Giese, 1959). The patterns of late winter / spring or summer reproduction observed in San Juan Channel, at least in part, very probably represent reproduction by northerly and southerly-distributed species, respectively.

Control of reproduction

While all reproductive processes are products of evolution, immediate control of gametogenesis and spawning is thought to be effected by physiological responses to environmental variables that serve as cues (Giese, 1959). These variables have been termed "proximal cues" to distinguish them from the more general selective pressures which shape reproductive patterns (or "ultimate cues"; see Giese and Pearse, 1974). A number of environmental variables have been suggested to control both gametogenic cycles and spawning, though the distinction between these processes has often been overlooked. Temperature and salinity changes or thresholds, lunar or tidal cycles, changes in quality or quantity of illumination, and increases in phytoplankton abundance have all been suggested to function as proximal cues (reviewed in Appendix A). The utility of these factors depends on their cyclic and predictable variation so that synchronous gametogenesis and spawning of conspecifics may result. In San Juan Channel salinity does not appear to vary with regularity, and the sampling schedule (2 wk intervals) probably obscured any lunar or tidal spawning periodicity. However, temperature, photoperiod and phytoplankton abundance (as plankton biomass) underwent annual cycles that may have affected gametogenesis or spawning. Because photoperiod affects temperature cycles and both interact to produce phytoplankton growth, these factors do not vary with complete independence.

Almost all peaks of larval abundance occurred during periods of rising temperature and plankton biomass (Fig. 22). Species spawning during late winter or early spring did so while daylength was increasing; larvae occurring during summertime were mostly spawned during periods of decreasing daylength. Though it is not possible to identify causative factors, it is notable that most late winter and springtime spawning occurred as temperature and plankton biomass began to rise from low winter levels, but well before the sharp springtime increases in plankton biomass (Fig. 4; see also Fernaux, 1965). Summertime spawning occurred during or just prior to peak levels of both temperature and plankton biomass. As mentioned above, a number of previous researchers have observed similar phenomena (Thorson, 1946; Sullivan, 1948; Bousfield, 1952-53; Hannerz, 1956; Lonning, 1963; Bhaud, 1967, 1972; Mileikovsky, 1970; Rasmussen, 1973; Falk-Petersen, 1982; Yokouchi, 1984), most of which are presumably controlled

by the direct effects of temperature on metabolism (Orton, 1920; see Korringa, 1957) and directly or indirectly, by seasonal cycles of phytoplankton production (reviewed by Giese, 1959; Giese and Pearse, 1974). Many of the periods of peak larval abundance were discrete, with few or no larvae of a given types occurring either before or after the peak occurrence (e.g., Figs. 10, 12). The discrete peaks of larval abundance presumably indicate relatively precise control of spawning periods. The data for the echinoid species, for which estimates of larval age can be made, do however indicate that S. franciscanus populations must have spawned a number of times both years (see Larval Abundances, below). Curiously, 4-armed plutei of S. franciscanus and S. droebachiensis occurred together in March of both years, though the major S. franciscanus spawnings occurred later. Perhaps some individuals of both species spawned in response to the same cues in March. McEuen (1986) has argued that some holothurian species in the San Juan Archipelago spawn during or shortly following prolonged periods (ca. 1 wk) of sunny weather, during periods of slack tide. If temperature or photoperiod synchronize gametogenic cycles, local cues such as bright sunlight, current strength, or increases in phytoplankton abundance might induce spawning (see Giese, 1959; Himmelman, 1981; Pearse and Eernisee, 1982; Appendix A).

In the present study, larval types (polychaetes, gastropods, lamellibranchs, cirripedes) present in high abundance for prolonged periods were those probably composed of a number of species which spawned consecutively. However, spawning periods of several months are not uncommon among invertebrate species (see Thorson, 1946; Giese, 1959) and some individual species may have been continuously present.

If thermal or phytoplankton cycles affect gametogenesis and spawning periodicity, it might be expected that variations in temperature or plankton biomass between years would cause similar variation in periods of larval abundance. During 1983, wintertime water temperatures were substantially warmer than in 1984 (ca. 2° C, Fig. 2). As a probable consequence, plankton biomass began its sharp increase in late April of 1983, almost a month earlier than in 1984. These interannual differences in temperature and plankton biomass cycles may have caused some taxa to spawn later in 1984. For example, both peaks in ophiopluteus abundance occurred somewhat later in 1984 than in 1983, though reasons for the delay of the fall peak are not clear since summertime differences

in plankton biomass or temperature between years were not marked. Among echinoplutei, the peak of S. droebachiensis abundance occurred on about the same date each year, but the major peak of S. franciscanus abundance was delayed about a month in 1984. Similarly, for planktotrophic holothurian and asteroid larvae the first major peak in abundance appeared about 2 weeks later in 1984 than in 1983. Curiously, as for the ophiuroids, the fall peak in cyphonautes abundance also occurred about a month later in 1984. These results indicate that the spawning of some taxa, at least, is controlled or facilitated by warmer temperatures or higher plankton (phytoplankton) biomass during some years. Similar interannual variations in the timing of larval peak abundances have also been observed by other workers (Thorson, 1946; Pyefinch, 1947; Quayle, 1952; Rees, 1954a, 1954b; Raymont and Carrie, 1964; Thiriot-Quievereux, 1968; reviewed in part by Thorson, 1950; Giese, 1959). As done here, such variations have usually been ascribed to interannual temperature and phytoplankton production differences.

Interannual temperature or plankton biomass differences may also account for the differing mean abundances of some larval types between years. All echinoderm larvae except lecithotrophic holothurians and asteroids had higher mean abundances during 1984, the colder year. Conversely, gastropod veligers, brachyuran zoeae, cirripede nauplii and ascidian tadpoles were more abundant during 1983. While these differences are statistically significant, they are difficult to evaluate because direct relationships between the observed temperatures or plankton biomass and adult fecundity or larval survival are not apparent. Similar fluctuations are not uncommon in other localities (citations of previous paragraph), and indeed, these variations form the basis for Thorson's (1950) characterization of reproduction via planktotrophic larvae as risky but occasionally rewarding (see also Strathmann, 1985, for a recent evaluation).

LARVAL POPULATION DYNAMICS

Peak abundances

The most abundant larvae to occur in the plankton were cirripede nauplii, which reached a peak abundance of almost 2600 individuals per cubic meter during spring of 1983. Lamellibranch veligers were also very abundant, reaching peak abundances of over

800 ind./m^3 during summertime. Even during periods of peak occurrence, all other larval types were much less common. Cirripedes and lamellibranchs clearly used the local plankton more extensively than did other taxa (Fig. 23), and it would not be surprising if cirripede nauplii and lamellibranch veligers both satiated their predators and substantially reduced food resources during periods of peak abundance (but see Jorgensen, 1981). In contrast, many types of lecithotrophic larvae were not found in the plankton samples at all, and those that were observed (ascidians, holothurians, asteroids) were found in relatively low numbers (Fig. 23). Neglecting any under-sampling of buoyant larvae, these abundances reflect adult population sizes and individual fecundities, as well as the duration of the planktonic stages. It would appear that species which produce lecithotrophic larvae have greatly reduced their use of the plankton as larval habitat (Thorson, 1950). The larval types and abundances other authors have observed vary greatly depending on local faunas, and there is little need to review their results in detail. As a contrasting example, however, Thorson (1946) found very few cirripede larvae, presumably because cirripede adult habitat is rare in the Baltic and Kattegat, but calculated peak abundances of 1.6 million lamellibranch veligers/m^3 in the Isefjord during one summer (see also Rasmussen, 1973; Jorgensen, 1981).

For some species it is possible to calculate order-of-magnitude estimates of the number of eggs produced by adult populations and to compare these figures with peak larval abundances. Although such calculations are subject to numerous uncertainties and sources of error, I have nevertheless estimated total egg production of the San Juan Channel population of the echinoid S. droebachiensis because of my interest in echinoid spawning and egg fertilization (Appendix A). If San Juan Channel is assumed to be a box-like trough 1.5×10^4 m long, 2.0×10^3 m wide and 140 m deep which is populated at a density of 12 ind./m^2 by adult S. droebachiensis (Shelford et al., 1935), of which half are females producing 10^6 eggs annually (Thompson, 1979), then a total of about 10^{14} eggs should be spawned in San Juan Channel each year. If these are homogeneously mixed in the water column, are not diluted or advected away, and all develop into 4-armed plutei, then 10^5 ind./m^3 should have been observed each spring about 4-14 days after spawning. The peak number of S. droebachiensis plutei actually observed was about 10 ind./m^3, or 4 orders of magnitude less than calculated. If all of the eggs were fertilized, minimum

instantaneous loss rates would be 0.65 / day (65% / day), much higher than those than those calculated for most larval types (below; reviewed by Strathmann, 1985). Though the calculation may be based on overestimates of adult density or egg production, plutei are geonegative and were probably more abundant near the surface than at depth (Appendix B), offsetting the above innaccuracies. In any case it is apparent that a large portion of the eggs presumably spawned were not observed as young larvae. Sources of this loss may be failure at fertilization (Appendix A), high embryonic and early larval mortality (Chapters III-VI), and dispersion or advection prior to sampling (below). However as noted above, it is not clear why S. franciscanus, which is less abundant than S. droebachiensis in San Juan Channel (Shelford et al., 1935), apparently produced more larvae than did S. droebachiensis. Calculated pre-larval losses for S. franciscanus would be somewhat lower than described above.

Loss from the plankton

For those taxa in which peaks of larval abundance probably represent spawning by single species, rates of decline from peak values were steep but not unexpectedly high. Apparent losses of larvae from the plankton (instantaneous loss rates; see Strathmann, 1985) were generally 3-12% per day as calculated from a logistic curve fit through the declining larval abundances of several taxa (cirripede nauplii, middle peak, 1984; brachyuran zoeae, 1983; echinoplutei, major peak, 1984). These losses are distinct from those calculated above because they cannot include failure at fertilization (Appendix A) or especially high rates of embryonic mortality (Chapter III), but they do include losses from all sources of larval mortality as well as any dilution or net movement away from (or to) the sampling station. Sources of mortality include predation and possibly starvation (see Korringa, 1957; Paulay et al., 1985), but as explained in Chapter III it is not at present possible to estimate daily mortality rates due to predation alone. Nonetheless at instantaneous mortality rates of 0.03 and 0.12 / day, 5% of a larval cohort would survive 100 and 25 days, respectively, or somewhat longer than required for development through metamorphosis for most planktotrophic larval types (Thorson, 1946, 1950). However, for those larval types which could be staged (e.g., echinoplutei) almost all larvae observed were younger stages. Thus estimates of daily loss include development from

younger to older stages (e.g., development of 4-armed into 6-armed plutei), but these older stages were rarely if ever observed. Additionally, at least in the case of echinoplutei, younger stages (4-armed plutei) resulting from a single spawning could not have persisted for about 30 days as was observed (i.e., largest peaks of Fig. 12); a series of spawnings must have contributed to the observed larval abundances. It is clear that a number of factors must have contributed to the observed rates of decline of larval populations, and it is not possible to partition these losses into their respective causes.

The nearly uniform lack of later larval stages may be accounted for by vertical and horizontal movement of larvae away from the sampling station. As suggested by Thorson (1964; reviewed in Appendix B), many larvae live at or near the surface when young and move to deeper water as they mature. Some vertical stratification of larvae probably occurs in San Juan Channel (see Sources of Variation, above), and ontogenetic vertical movements of larvae away from the surface may account for some of the decline in larval abundance. However, the curves for all the larval types exhibit similar rates of decline, and at least some of these larvae probably do not undergo ontogenetic vertical migrations (reviewed by Banse, 1964; Appendix B). A major additional source of loss was probably advection. As discussed previously, currents in the San Juan Archipelago are strong and entail a net flow of water south from the Strait of Georgia into the Strait of Juan de Fuca. At a net seaward flow of 15 cm/s (Thompson, 1981), the water in San Juan Channel could be replaced by Strait of Georgia water every 36 hours; this calculation neglects tidal flushing. Because the volume of water both in the Strait of Georgia and the Strait of Juan de Fuca is high relative to benthic surface area, abundance of larvae in waters entering the San Juan Archipelago from either the north or south is probably relatively low. The high benthic surface area to water volume ratio in the San Juan Archipelago probably results, following local spawning, in high larval densities (particularly of hard-botton species) which persist only until advected into the Strait of Juan de Fuca. For those few larval types for which larval age can be estimated from their stage of development (e.g., echinoids), this argument probably accounts for near absence of later-stage larvae in the plankton samples. Considering all of the potential sources of loss, the 0.03-0.12/day instantaneous rates of loss observed for younger larvae are remarkably low, and indeed are somewhat lower than those calculated for most other invertebrate larvae in the

plankton (reviewed by Strathmann, 1985).

Juvenile recruitment

The only larvae identified in the plankton samples as presumably "competent" to settle and metamorphose were ascidian tadpole and cirripede cyprid larvae. It is probable, however, that many cyphonautes larvae (as described by Atkins, 1955a), and some lecithotrophic holothurian and asteroid larvae were also competent. Additionally, a small fraction of the polychaete and lamellibranch larvae were late-stage larvae, though none of these were identified as competent to settle and metamorphose. No megalops or competent planktotrophic echinoderm larvae were observed.

The lack of late-stage larvae in the samples may in part result from ontogenetic vertical migrations and advection into the Strait of Juan de Fuca as discussed above. These arguments are apparently not tenable for competent cyphonautes larvae, which require several weeks to develop and yet were fairly common in the plankton samples.

Because the plankton tows sampled a very small percentage of the volume of San Juan Channel, it is not clear if poor larval supply might limit population sizes of adult invertebrates in San Juan Channel. However, the occurrence in some local areas of the San Juan Archipelago of abundant populations of juvenile invertebrates (e.g., "Barnacle Rock" in East Sound, Orcas Island; Fig. 1) probably indicates that late-stage larvae are retained in some locales, resulting in heavy recruitment. For example in East Sound, Emlet (1985) found both early and late-stage echinoplutei of Dendraster excentricus in much higher abundances than they occur in San Juan Channel (see also Appendix B). At least some of these larvae were presumably spawned within East Sound and retained locally throughout their development. Such retention probably does not occur in San Juan Channel.

In contrast with the present study, most larvae that Thorson (1946) observed were late-stage precompetent larvae; he rarely observed young stages in his samples. Competent larvae were presumably rare because they had metamorphosed, and Thorson (1946) suggested that young stages were not present because most larvae in his samples originated in the Kattegat and were advected towards the Baltic, passing his sampling station only after several days or weeks of development. Hydrographic differences between study sites thus can have profound effects on the larval fauna observed in

samples, and should have equally important biological consequences for larvae (cf. Banse, 1964; Strathmann, 1982).

COMPARISON WITH JOHNSON (1932)

A number of previous researchers (see Introduction) have examined temporal patterns of abundance of invertebrate larvae in the plankton, and all of these studies stongly reflect local climatic, geologic and hydrographic conditions, as well as the local faunas. For this reason I have not reviewed the results of the various surveys in detail, but have discussed their general conclusions in the foregoing sections. However, Johnson (1932) did provide cursory documentation of annual occurrences of invertebrate larvae in Friday Harbor, where the present study was conducted, as part of a more general study. His results are thus directly applicable to the present study, and are reviewed in detail below.

Johnson (1932) took qualitative plankton samples by net during portions of 1923-29 in Friday Harbor, about 2 km from the San Juan Channel site where the present study was conducted. His table of results is reproduced here for ease of comparison (Table III). Johnson found polychaete, gastropod and lamellibranch larvae to be most common during the same general portion of the year as observed in my study. Cirripede nauplii occurred in one or two peaks rather than three as I observed, and very few cyprids were found in either study. Johnson only found cyphonautes larvae in late summer and fall; the spring and summertime cyphonautes I observed were apparently unrepresented in his samples. Johnson found a few echinoplutei in March and fewer through June, in very rough agreement with my results. Fall peaks of ophioplutei occured in both studies, and the February peak abundance of ophioplutei in my data was weakly reflected in Johnson's samples as well. Finally, Johnson found lecithotrophic holothurian larvae during the same general period as in the present study. Johnson did not record brachyuran, ascidian, or planktotrophic holothurian or asteroid larvae from his samples.

Although Johnson's (1932) observations differ in numerous particulars from the present work and contain essentially no information on larval population dynamics, these differences can probably be ascribed to the small numbers of larvae which Johnson observed (generally <10 individuals of a given larval type per month). Nonetheless, the

general correspondence between studies in seasons of larval presence is good, and I believe this concordance is strong evidence that the broader patterns described in both studies are accurate.

Table 1. Dates of collection of samples sorted, time and tidal stage of collection (LS, low slack; HS, high slack tide), duration of the tows, volume of plankton filtered as calculated from the flowmeter, portion sorted, and conversion factors to number of larvae per cubic meter of plankton per larva directly observed in the subsamples.

Collection Date (1983)	Time of Day	Tidal Stage	Duration Tow (min)	Vol. (m3) Filtered	Portion Sorted	Conversion Factors
1/3	1314	LS	10	43.00	1/4	0.09
1/17	1200	LS	10	44.00	1/4	0.09
1/31	1300		10	41.50	1/8	0.19
2/14	1130	LS	10	48.00	1/8	0.16
2/25	1530	HS	10	42.00	1/16	0.38
2/25	1530	HS	10	43.30	1/16	0.37
3/14	1100	LS	10	37.20	1/32	0.86
3/14	1100	LS	10	37.20	1/32	0.86
3/14	1100	LS	10	34.30	1/32	0.93
3/14	1100	LS	10	34.30	1/32	0.93
3/14	1100	LS	10	33.10	1/32	0.97
3/14	1100	LS	10	33.10	1/32	0.97
3/28	1030	LS	10	43.10	1/32	0.74
3/28	1030	LS	10	36.60	1/32	0.87
4/11	930	LS	10	32.30	1/32	0.99
4/11	930	LS	10	36.40	1/32	0.86
4/25	800	Ebb	10	30.60	1/64	2.09
4/25	800	Ebb	10	28.80	1/64	2.22
4/25	1100	LS	10	33.90	1/64	1.89
4/25	1100	LS	10	26.90	1/64	2.37
4/25	1400	Flood	10	30.60	1/64	2.09
5/9	1042	LS	10	13.50	1/32	2.36
5/23	1000	LS	5	7.40	1/32	4.34
6/6	900	LS	5	10.00	1/32	3.19
6/20	945	LS	5	13.50	1/32	2.36
6/20	945	LS	5	13.20	1/32	2.42
7/5	1500	HS	2.5	3.50	1/32	8.08
7/18	1420	HS	2.5	6.90	1/16	2.31
8/1	1200	HS	5	7.10	1/16	2.24
8/15	1310	HS	2.5	5.60	1/16	2.85
8/29	1020	HS	2.5	5.70	1/16	2.8
9/12	1150	HS	2.5	5.90	1/16	2.68
9/26	930	HS	2.5	6.80	1/16	2.35
10/10	945	HS	2.5	9.70	1/16	1.65
10/24	845	HS	5	14.00	1/16	1.14
11/7	1240	HS	5	16.70	1/8	0.48
11/21	1110	LS	10	31.60	1/8	0.25
12/5	1140	HS	10	30.40	1/8	0.26
12/21	1145	HS	10	32.90	1/8	0.24

Table I (Continued).

Collection Date (1984)	Time of Day	Tidal Stage	Duration Tow (min)	Vol. (m3) Filtered	Portion Sorted	Calculated Ind./m3
1/2	1600	HS	10	36.90	1/8	0.22
1/17	930	HS	6	32.90	1/4	0.12
1/17	930	HS	6	32.90	1/4	0.12
1/17	930	HS	Vertical	8.90	1/4	0.45
1/17	930	HS	Vertical	9.90	1/4	0.4
1/30	1010	HS	10	30.10	1/4	0.13
2/13	1200	HS	10	29.50	1/4	0.13
2/29	945	LS	10	29.00	1/4	0.13
3/12	1010	HS	10	29.10	1/16	0.55
3/26	1140	HS	10	11.40	1/32	2.8
4/10	1000	HS	5	14.00	1/32	2.29
4/23	1600	LS	5	22.30	1/16	0.72
5/8	1340	LS	4	15.20	1/32	2.11
5/8	1340	LS	4	15.10	1/32	2.13
5/8	1330	LS	Vertical	2.60	1/8	3.03
5/8	1330	LS	Vertical	2.50	1/8	3.16
5/21	1100	LS	5	13.20	1/32	2.42
6/4	1500	LS	5	6.90	1/32	4.62
6/18	1500	LS	5	7.40	1/32	4.34
7/2	1410	LS	2.5	9.00	1/32	3.55
7/16	1345	LS	2.5	4.00	1/32	8.08
7/30	1410	LS	2.5	5.00	1/32	6.39
8/13	1300	HS	2.5	9.30	1/16	1.71
8/24	930	LS	2.5	3.70	1/16	4.28
9/11	1200		5	13.00	1/32	2.46
9/11	1200		5	11.50	1/32	2.77
9/11	1200		Vertical	2.20	1/16	7.27
9/11	1200		Vertical	2.60	1/16	6.06
9/24	1050	LS	5	15.60	1/32	2.05
10/8	1050	LS	5	15.00	1/16	1.07
10/22	1030	LS	5	9.60	1/16	1.67
11/5	830	LS	10	21.30	1/16	0.75
11/20	800	LS	10	20.00	1/16	0.8
12/3	1330	HS	10	25.50	1/16	0.63

Table II. Categorization of larval types by seasonal abundance in the plankton. Triple asterisks indicate periods of peak abundance, single asterisks indicate periods of minor abundance.

	Late Winter (Feb-Mar)	Spring (Apr-May)	Spring-Summer (Jun-Jul)	Late Summer (Aug-Sep)
Polychaeta	***		***	***
Gastropoda	*		***	***
Lamellibranchia			***	*
Bryozoa			***	*
Cirripedia	***	***	***	
Brachyura	***	***		
Echinoidea	***	***	*	
Ophiuroidea	***			***
Auricularias and Bipinnarias	***	***		
Lecithotrophic echinoderm larvae	***	*		
Tadpole larvae	*	*	*	*

Table III. Average monthly distribution of various larvae (directly from Johnson, 1932). Symbols: -, no sample; blank, no larvae present; +, larvae present but not counted; number, number observed; VA, very abundant but not counted; A, abundant but not counted; C, common but not counted; F, frequent but less than common and not counted.

SPECIES	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
Barnacle nauplii												
1923-24	7	2	+		+	+	-	24	14	-	-	-
1926-27	+	+				+	+	A	C	F	-	-
1927-28	2	1	1			1	80	5	14	10	7	4
1928-29	2	+		+		+	20	6	17	2	1	+
Cyphonautes larvae												
1923-24	4	5	5				-			-	-	-
1926-27	F	F	C	+	+	+		+			-	-
1927-28	4	6	11	6	1				+	1	1	1
1928-29	3	5	3	1	+		+		+	+	+	1
Echinoplutei												
1923-24							-	1		-	-	-
1926-27								+	+		-	-
1927-28							4	+	1	1		
1928-29							+	+	1	+		+
Gastropod larvae												
1923-24	6	6	2	+	1	1	-	2	2	-	-	-
1926-27	+	+	+	+	+	+	+	+	+	+	-	-
1927-28	10	8	4	2	2	2	3	2	2	1	2	2
1928-29	2	1	1	+	+	+	+	1	1	1	2	2
Holothurian larvae												
1923-24							-	C		-	-	-
1926-27							VA					
1927-28							VA	F	C			
1928-29							VA	C	A	F		
Ophioplutei												
1923-24	3	1					-	+		-	-	-
1926-27	+	+	+								-	-
1927-28	3	2	1			+	1			1	+	2
1928-29	2	1	+				+				+	2
Lamellibranch larvae												
1923-24	13	10	11	1	2	4	-	5	23	-	-	-
1926-27	+	C	F	+	+	+	+	+	+	+	-	-
1927-28	10	23	17	9	9	7	6	5	12	10	20	27
1928-29	8	7	4	2	3	3	2	1	6	19	18	10
Polychaete larvae												
1923-24	5	3	1		+		-	3	1	-	-	-
1926-27	F	+	F	+	+		+	F	+	+	-	-
1927-28	9	6	5	1	+	+		F	+	+	-	-
1928-29	5	4	1	+	+	+	1	+	2	3	4	4

Figure II-1. Map of the San Juan Archipelago, Washington. The study was conducted at Friday Harbor Laboratories (FHL), San Juan Island, and sampling was conducted 20-200 m northwest of the Reid Rock Buoy (arrow). Not shown is the Washington mainland and assorted islands to the east of Rosario Strait, and Vancouver Island to the west of Haro Strait. The Strait of Georgia borders the north, and the Strait of Juan de Fuca lies to the south of the Archipelago.

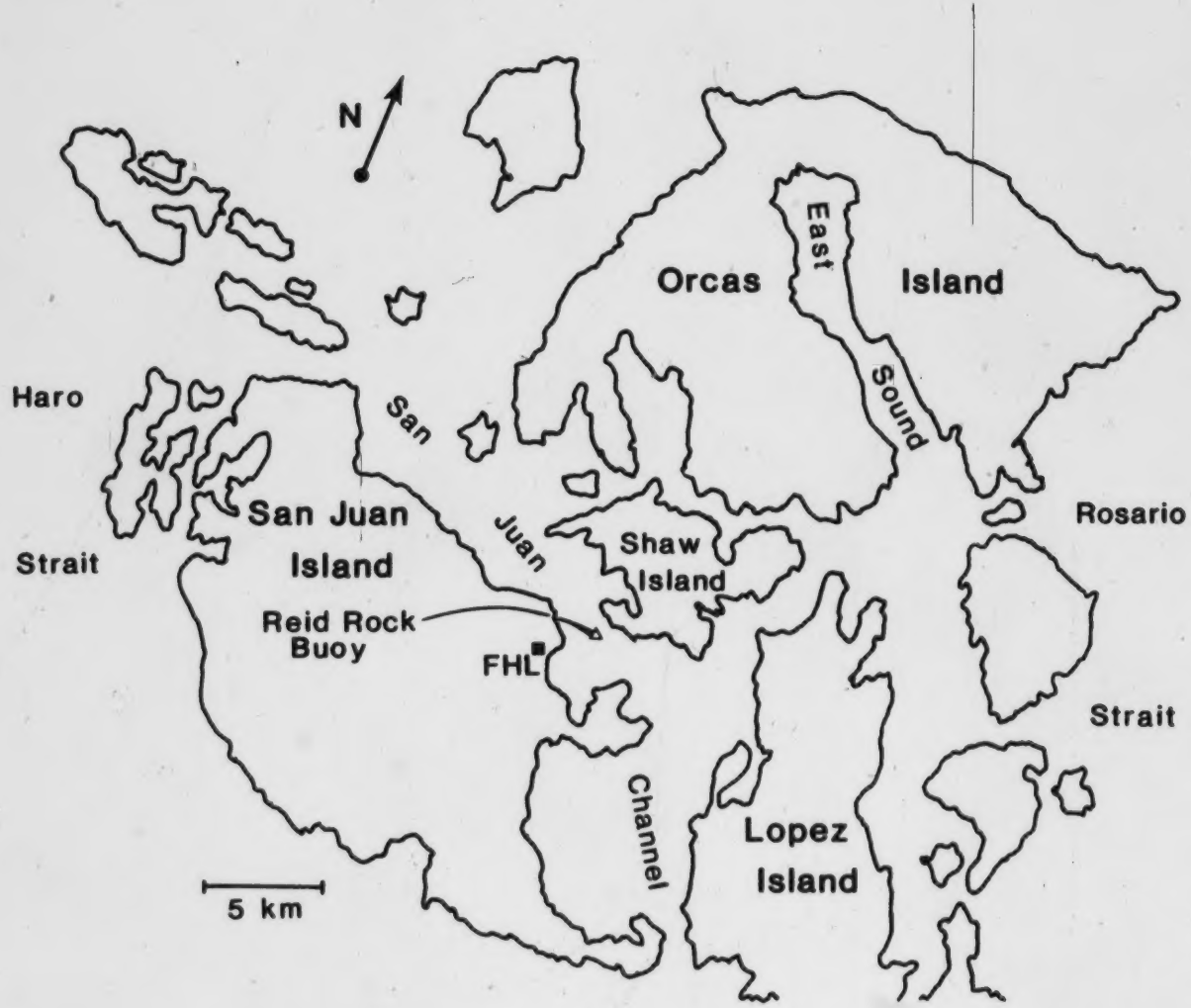
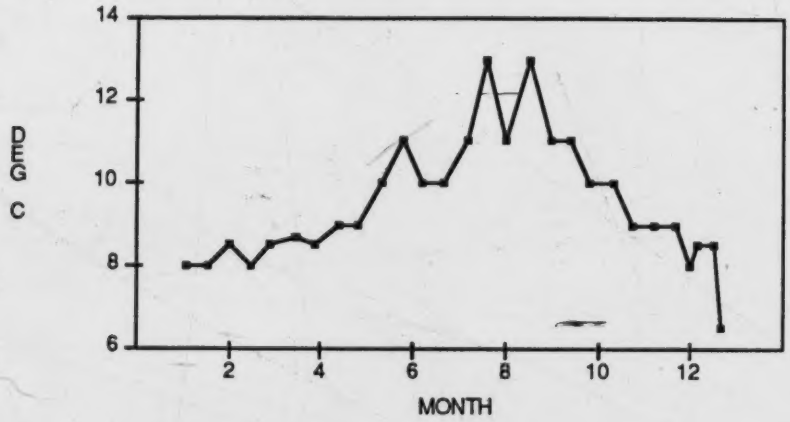

N
Orcas
Island
East
Sound
Haro
Strait
San
Juan
Island
San Juan
Island
Shaw
Island
Rosario
Strait
Reid Rock
Buoy
FHL
Channel
Lopez
Island
5 km

Figure II-2. Temperature (degrees C) of surface water in San Juan Channel throughout 1983 (A) and 1984 (B). In 1983 mean temperature was 9.6° with a range of 5.5°, in 1984 mean temperature was 8.8° with a range of 4.8°.

A. Temperature, 1983



B. Temperature, 1984

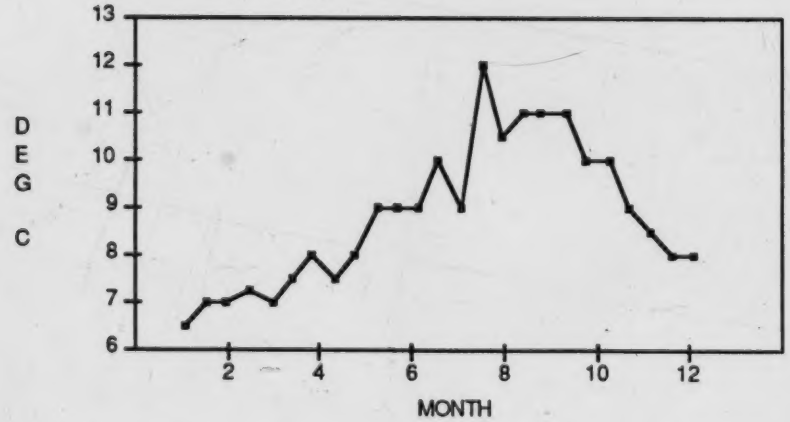
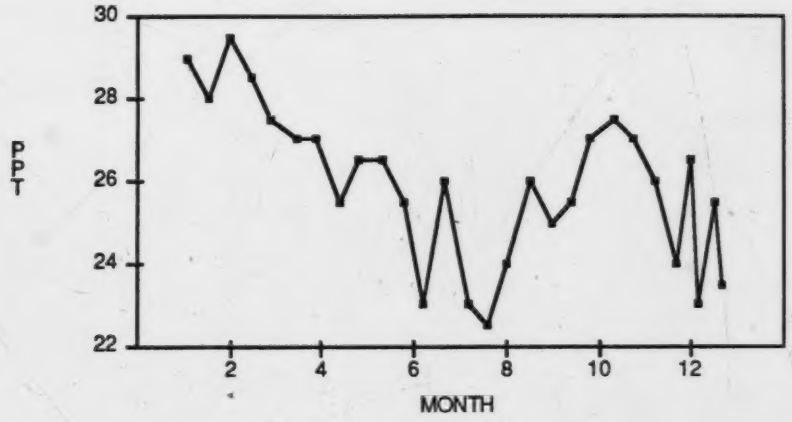


Figure II-3. Salinity of surface water in San Juan Channel throughout 1983 (A) and 1984 (B). Mean salinity in 1983 was 25.9 ppt with a range of 7.0 ppt; in 1984 mean salinity was 27.5 with a range of 12.0 ppt. However, a salinity meter became unreliable and gave erratic readings in late 1983 before discovery.

A. Salinity, 1983



B. Salinity, 1984

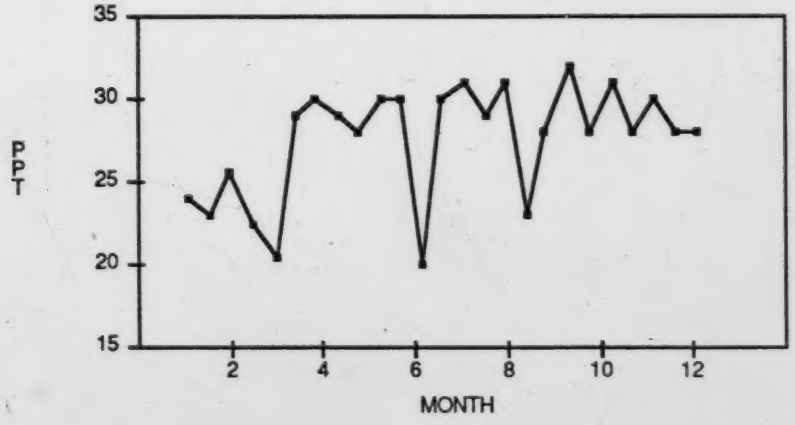
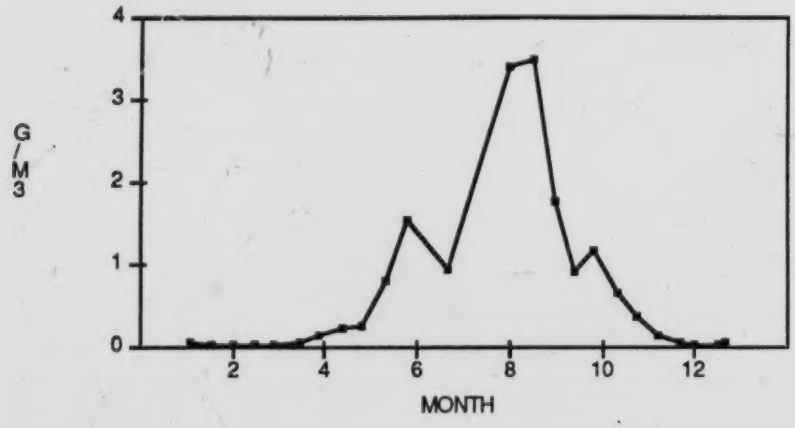


Figure II-4. Planktonic biomass, standardized to biomass per cubic meter of water, throughout 1983 (A) and 1984 (B). During winter the planktonic samples consisted largely of zooplankton, but biomass during spring, summer and fall was predominantly phytoplankton.

A. Plankton biomass, 1983



B. Plankton biomass, 1984

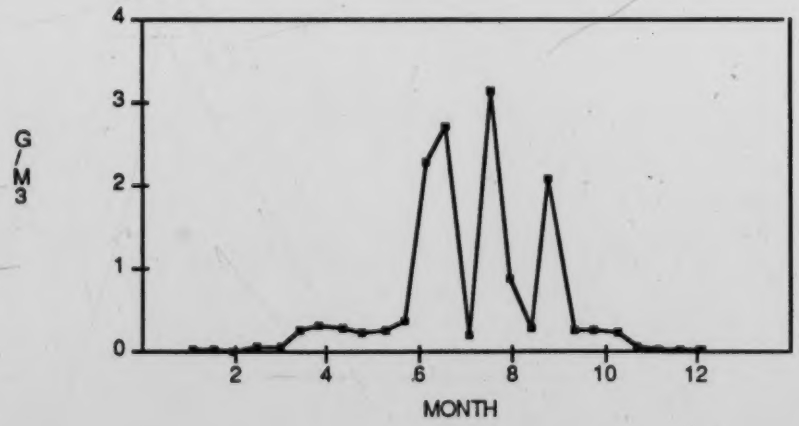
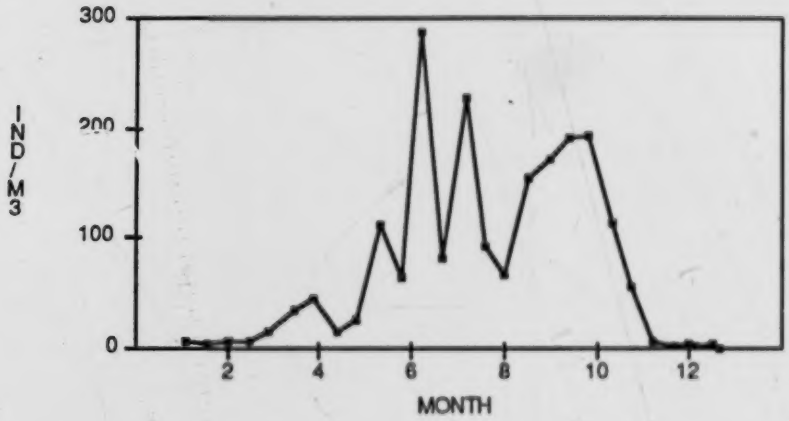


Figure II-5. Abundance of polychaete trochophores throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Polychaete trochophores, 1983



B. Polychaete trochophores, 1984

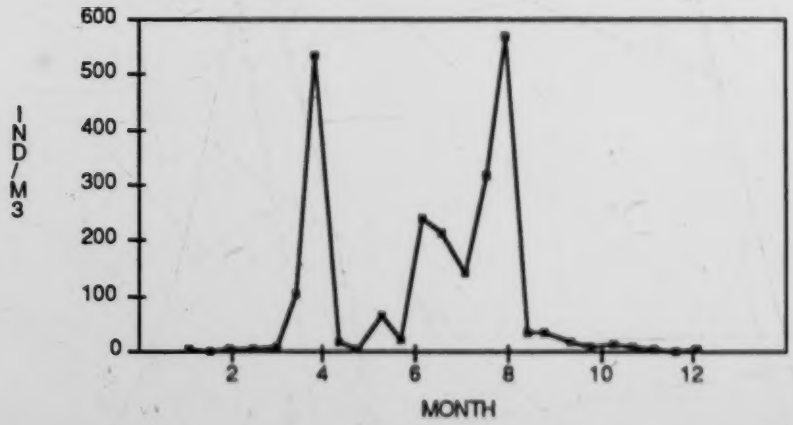
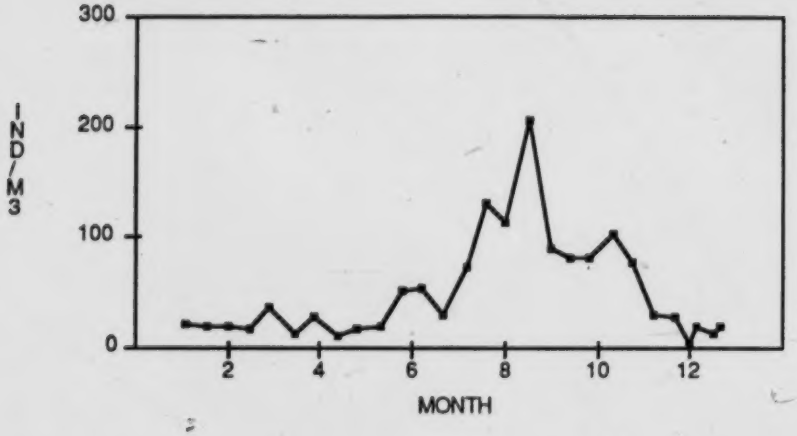


Figure II-6. Abundance of gastropod veligers throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Gastropod veligers, 1983



B. Gastropod veligers, 1984

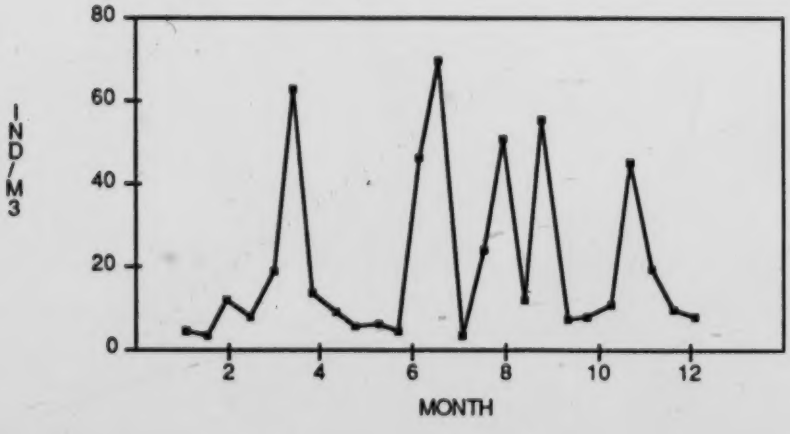
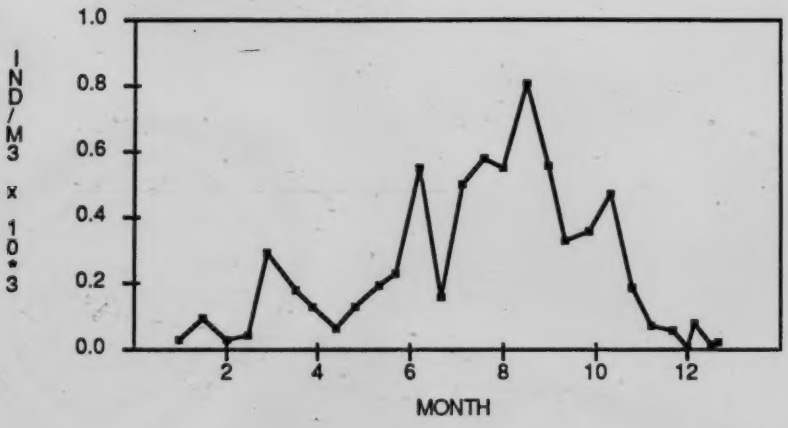


Figure II-7. Abundance of lamellibranch veligers throughout 1983 (A) and 1984 (B). Counts have been standardized and are expressed as numbers of larvae per $m^3 \times 10^3$; ordinates are to the same scale.

A. Lamellibranch veligers, 1983



B. Lamellibranch veligers, 1984

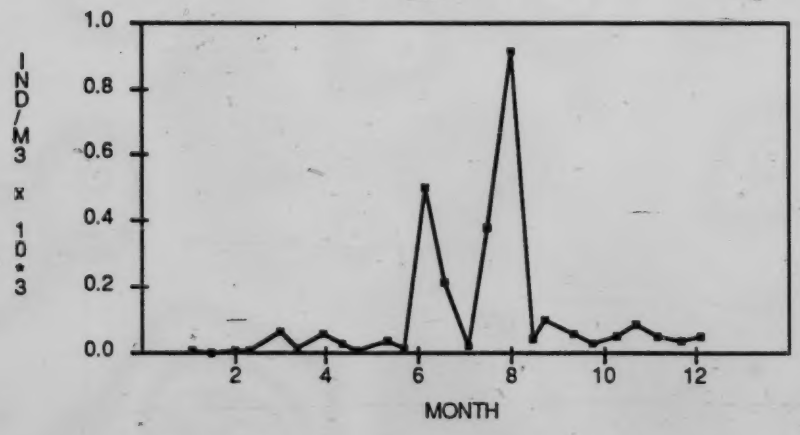
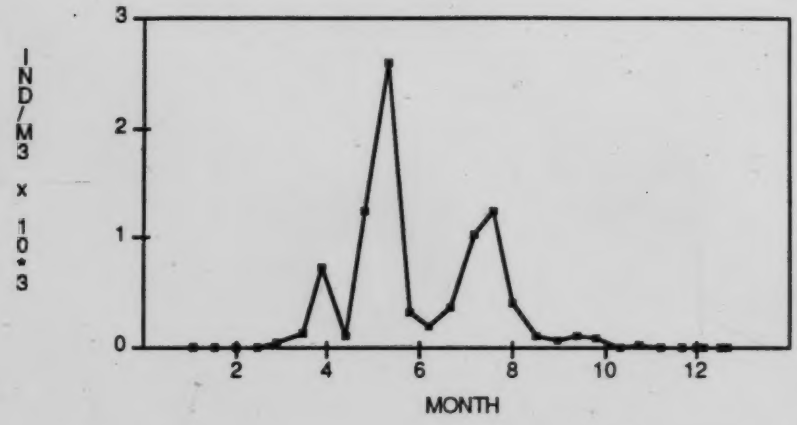


Figure II-8. Abundance of cirripede nauplii throughout 1983 (A) and 1984 (B). Counts have been standardized and are expressed as numbers of larvae per $m^3 \times 10^3$; note that the ordinates are not to the same scale.

A. Cirripede nauplii, 1983



B. Cirripede nauplii, 1984

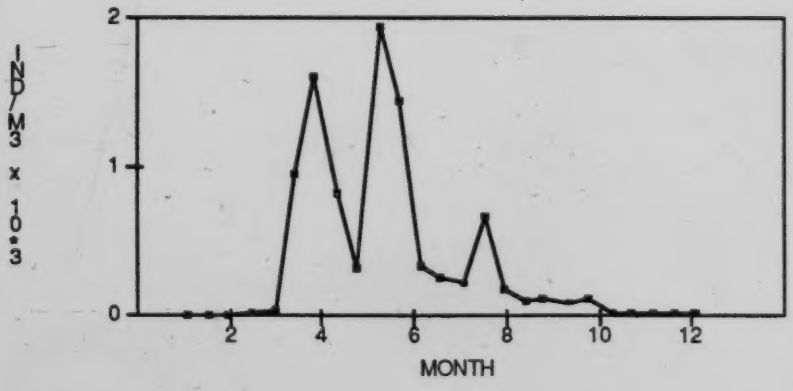
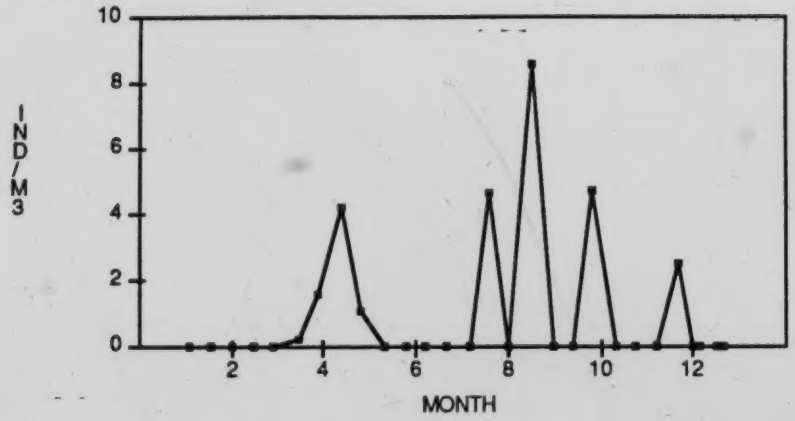


Figure II-9. Abundance of cirriped cyprids throughout 1983 (A) and 1984 (B). Cyprid abundances were so low that these data can be taken to indicate little more than presence or absence. Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Cirripede cyprids, 1983



B. Cirripede cyprids, 1984

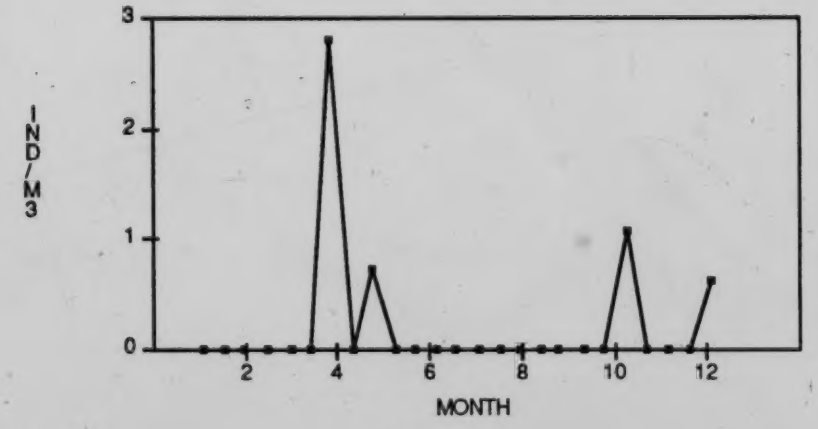
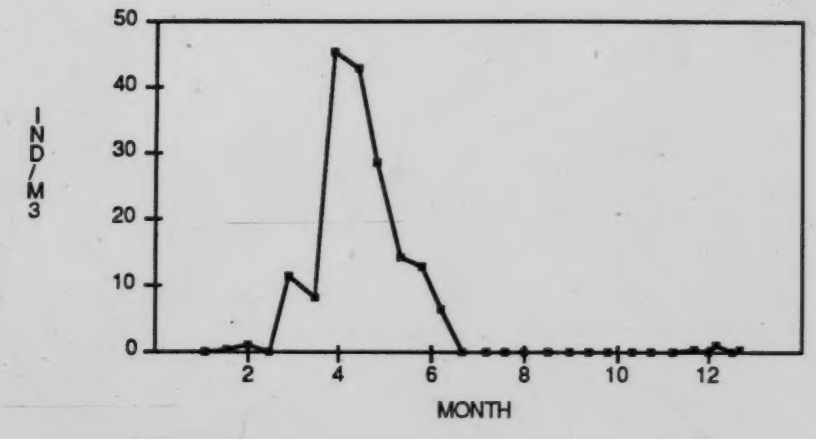


Figure II-10. Abundance of brachyuran zoeae throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Brachyuran zoeae, 1983



B. Brachyuran zoeae, 1984

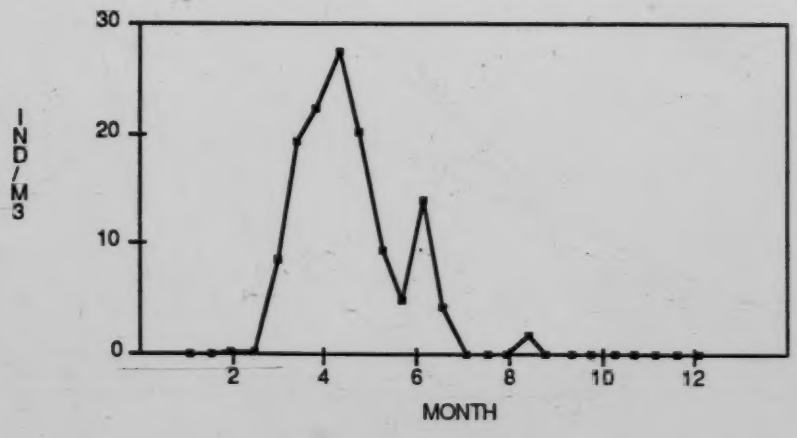
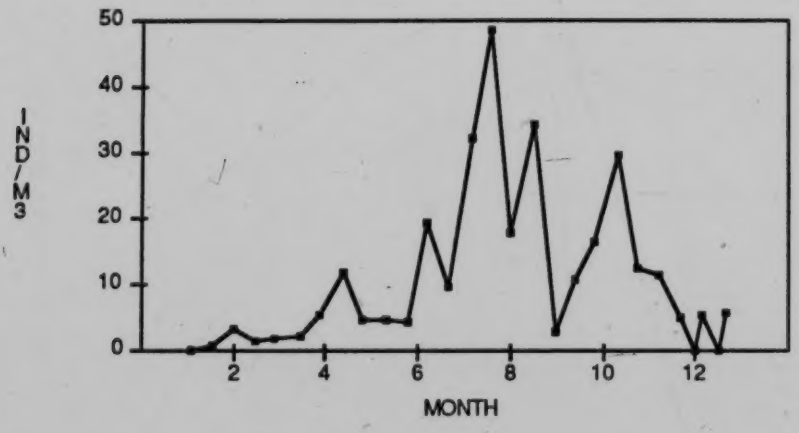


Figure II-11. Abundance of bryozoan cyphonautes larvae throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Bryozoan cyphonautes, 1983



B. Bryozoan cyphonautes, 1984

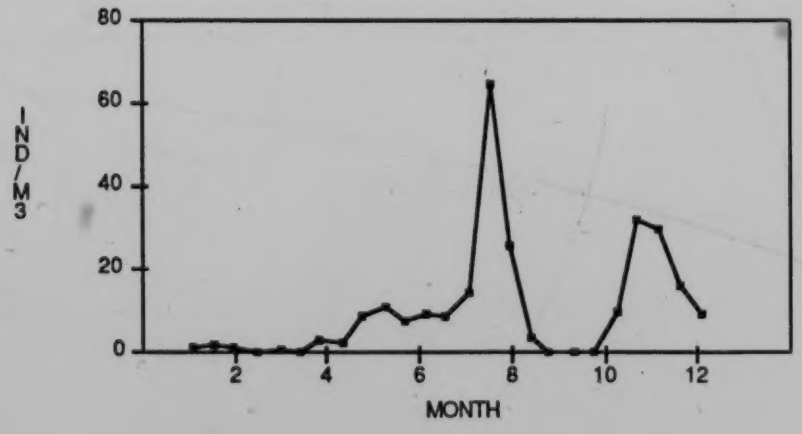
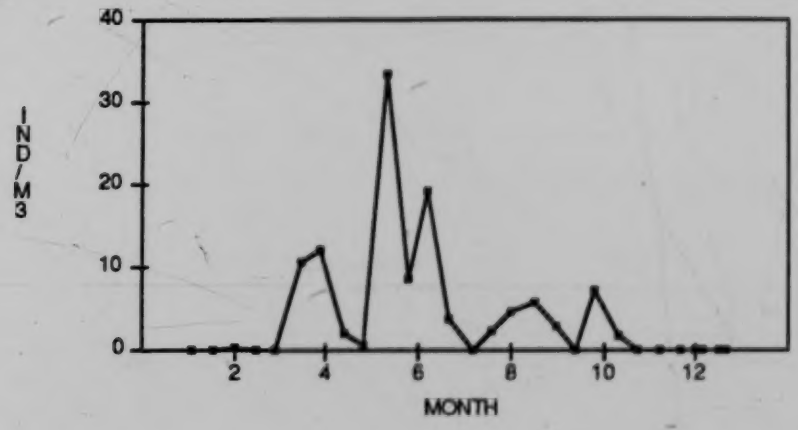


Figure II-12. Abundance of echinoid pluteus larvae throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Echinoid plutei, 1983



B. Echinoid plutei, 1984

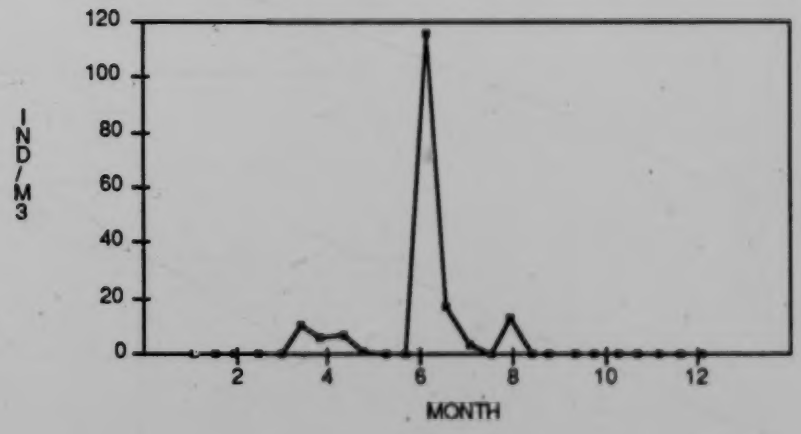
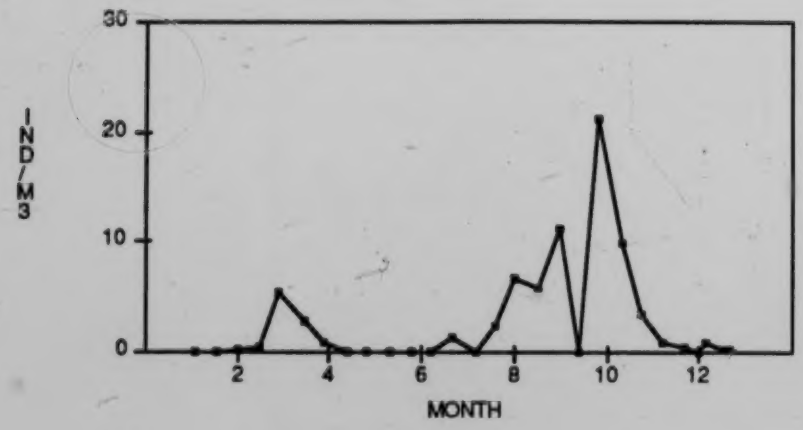


Figure II-13. Abundance of ophiuroid pluteus larvae throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; the ordinates are to the same scale.

A. Ophiuroid plutei, 1983



B. Ophiuroid plutei, 1984

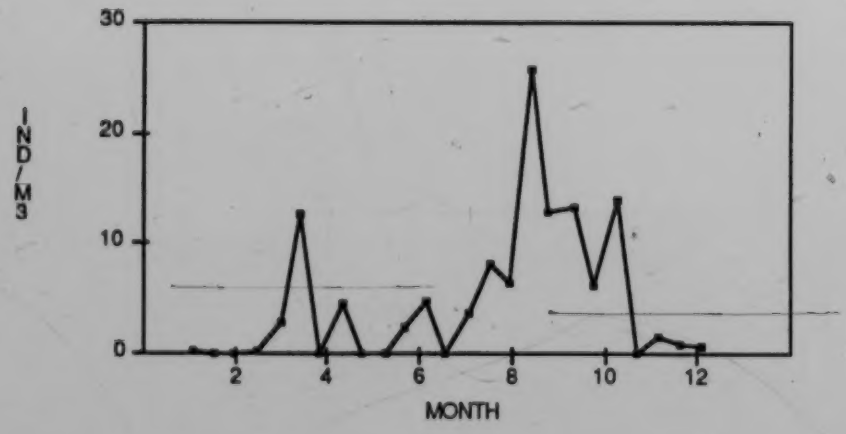
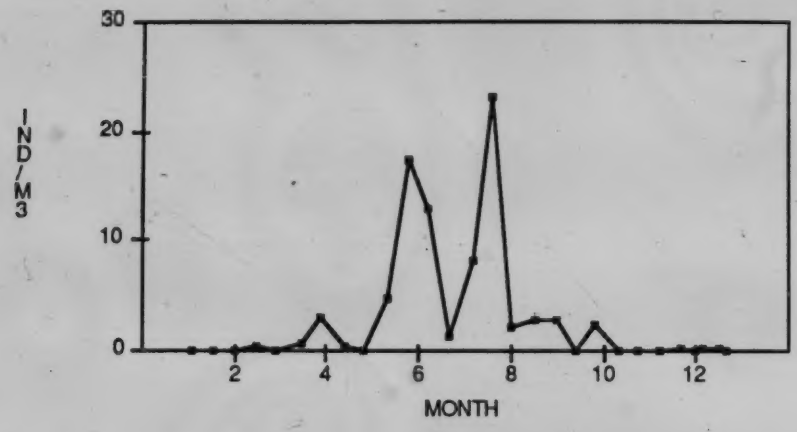


Figure II-14. Abundance of planktotrophic holothurian auricularias and asteroid bipinnarias throughout 1983 (A) and 1984 (B). Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Planktotrophic holothurian and asteroid larvae, 1983



B. Planktotrophic holothurian and asteroid larvae, 1984

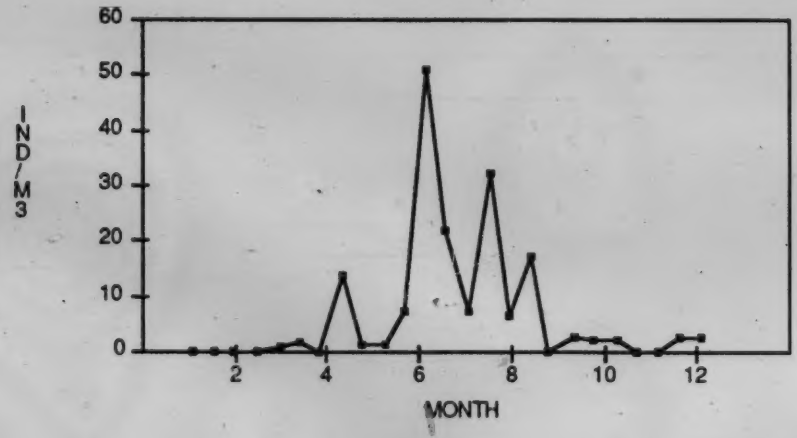
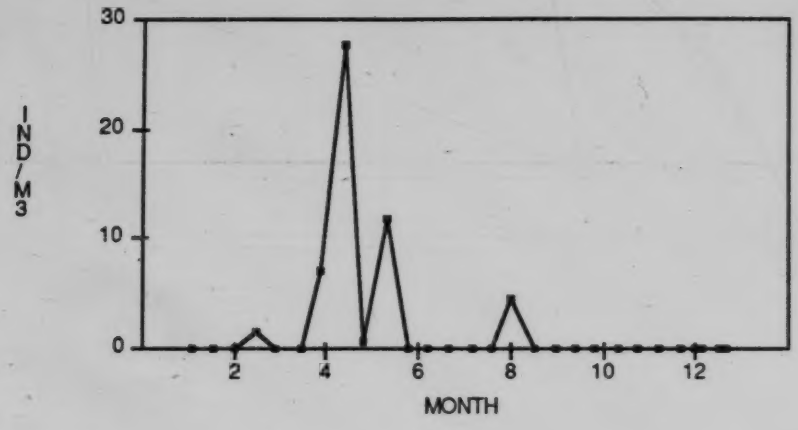


Figure II-15. Abundance of lecithotrophic holoturian and asteroid larvae throughout 1983 (A) and 1984 (B). Because most of these larvae float at the water surface they were sampled poorly by the net; the data can be taken to indicate larval presence or absence. Counts were standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Lecithotrophic holothurian and asteroid larvae, 1983



B. Lecithotrophic holothurian and asteroid larvae, 1984

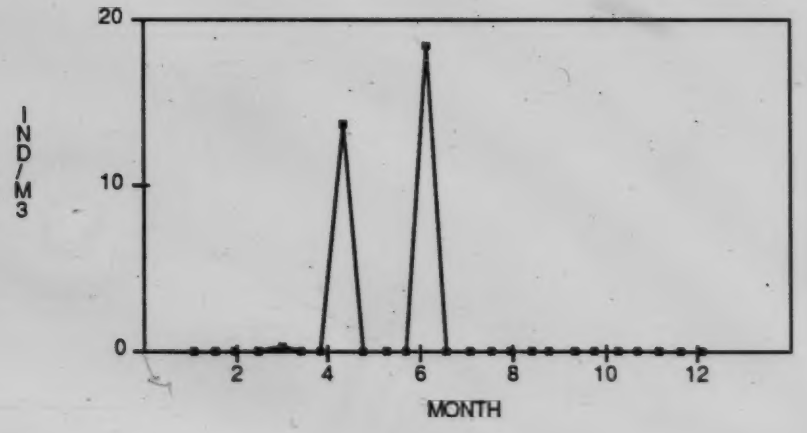
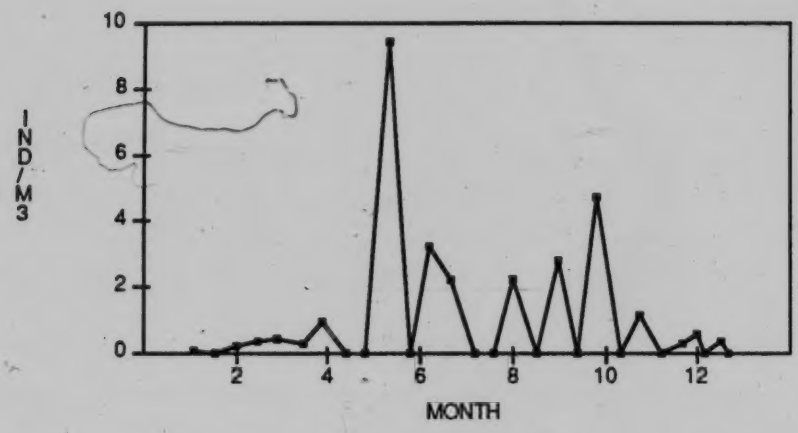


Figure II-16. Abundance of ascidian tadpole larvae throughout 1983 (A) and 1984 (B). So few tadpoles were observed that these data can be taken to indicate larval presence or absence. Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale.

A. Ascidian tadpole larvae, 1983



B. Ascidian tadpole larvae, 1984

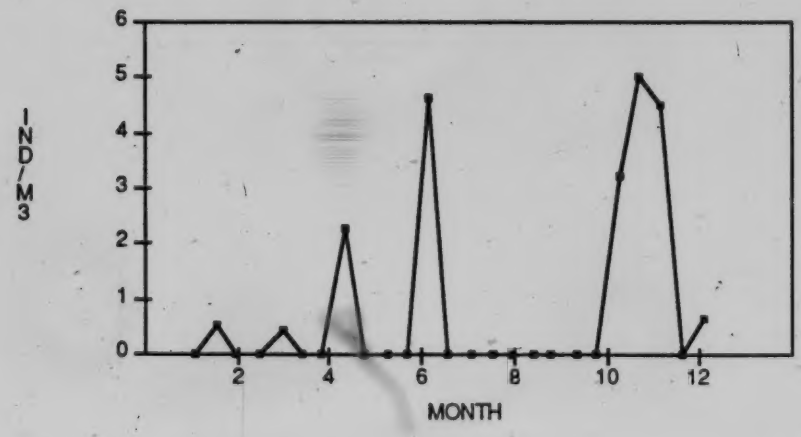


Figure II-17. Counts of the 6 most abundant larval types in 6 replicate surface tows taken on 3/14/83 (Table I). Variation in numbers of a given larval type sampled between tows was considerable (see text), but there was no significant effect of tow on the counts (Friedman's Test, $P>0.5$). Legend to the abcissa is: Poly, Polychaete trochophores; Lam, Lamellibranch veligers; Gast, Gastropod veligers; Cirrip, Cirripede nauplii; Brachy, Brachyuran zoeae; Echino, Echinoplutei.

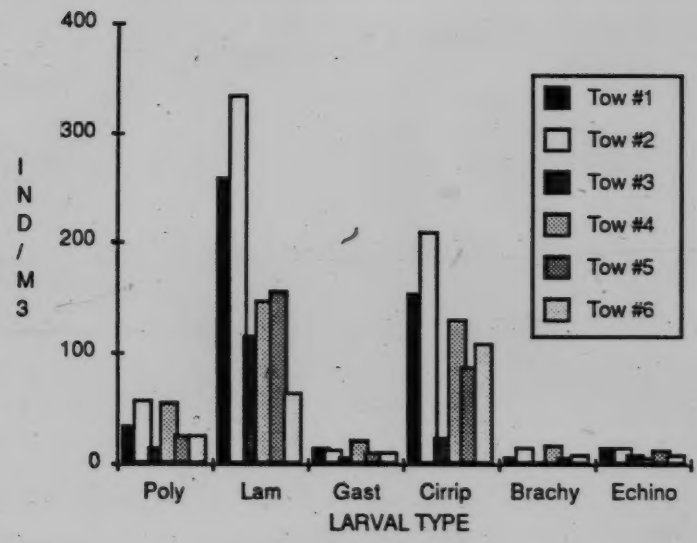
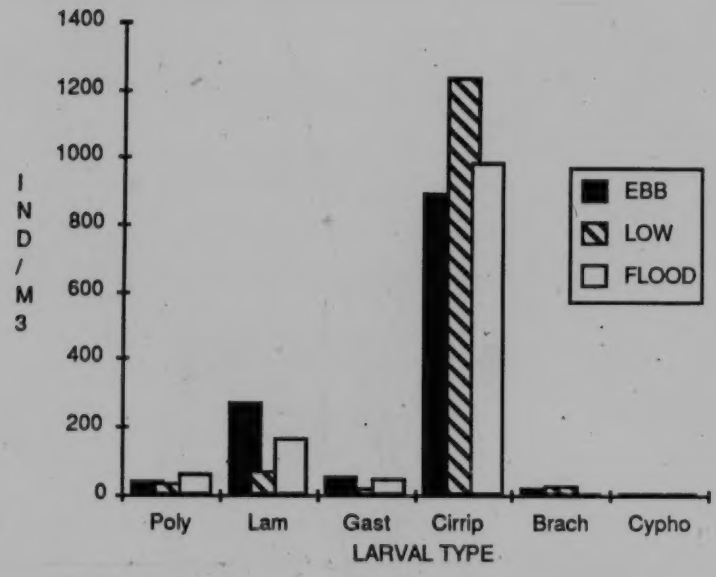

400
300
200
100
0
IND/M3
Tow #1
Tow #2
Tow #3
Tow #4
Tow #5
Tow #6
Poly
Lam
Gast
Cirrip
Brachy
Echino
LARVAL TYPE

Figure II-18. Abundances of larval types during three tidal stages during daytime on 4 / 25 / 83. Data for all larvae observed are presented in (A), while the data for cirripede nauplii have been excluded from (B) so that differences between the less abundant larvae are apparent. Counts have been standardized to numbers of larvae per m^3; values for ebb and low slack tide are means of 2 replicate tows, values for flood tide are single data; note that the ordinates are not to the same scale. Legend for the abcissa is: Poly, Polychaete trochophores; Lam, Lamellibranch veligers; Gast, Gastropod veligers; Cirrip, Cirripede nauplii; Brach, Brachyuran zoeae; Cypho, Cyphonautes larvae.

A. Tidal stages, cirripede nauplii included



B. Tidal stages, without cirripede data

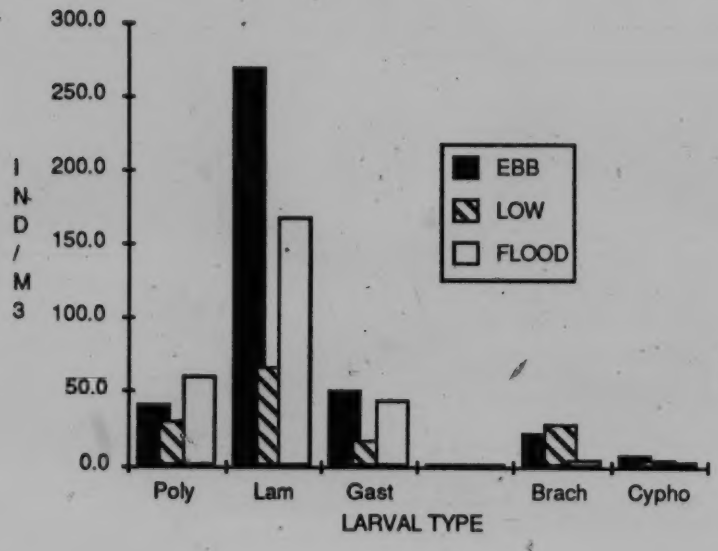


Figure II-19. Abundances of larval types observed in surface and vertical (0-80 m) hauls taken during daytime on 1/17/84. Counts have been standardized to numbers of larvae per m^3. Legend for the abcissa is: Poly, Polychaete trochophores; Lam, Lamellibranch veligers; Gast, Gastropod veligers; Cirrip Cirripede nauplii; Cypho, Cyphonautes larvae.

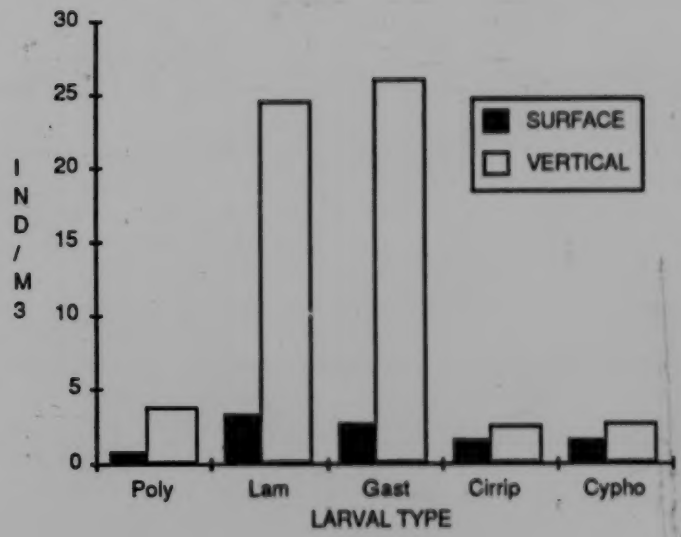
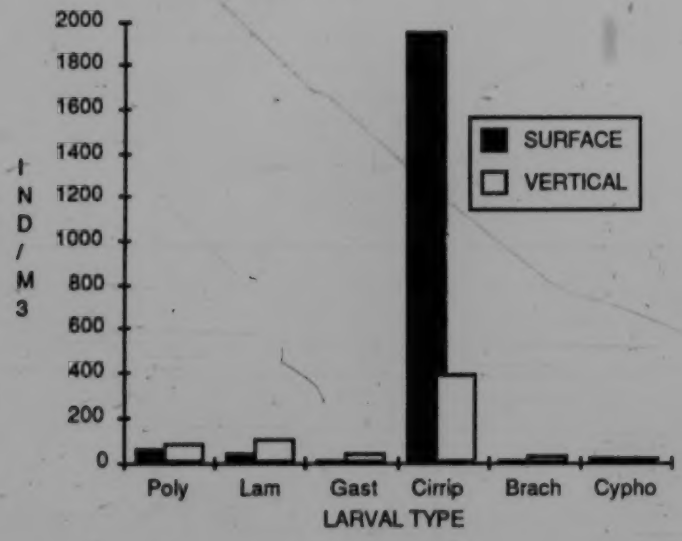

30
25
20
15
10
5
0
IND/M3
SURFACE
VERTICAL
Poly
Lam
Gast
Cirrip
Cypho
LARVAL TYPE

Figure II-20. Abundances of larval types observed in surface and vertical (0-80 m) hauls taken during daytime on 5/8/84. Data for all larvae observed are presented in (A), while the data for cirripede nauplii have been excluded from (B) so that differences between the less abundant larval types are apparent. Counts have been standardized to numbers of larvae per m^3; note that the ordinates are not to the same scale. Legend to the abcissa is: Poly, Polychaete trochophores; Lam, Lamellibranch veligers; Gast, Gastropod veligers; Cirrip, Cirripede nauplii; Cypho, Cyphonautes larvae.

A. Surface and vertical hauls, cirripede nauplii included



B. Surface and vertical hauls, without cirripede data

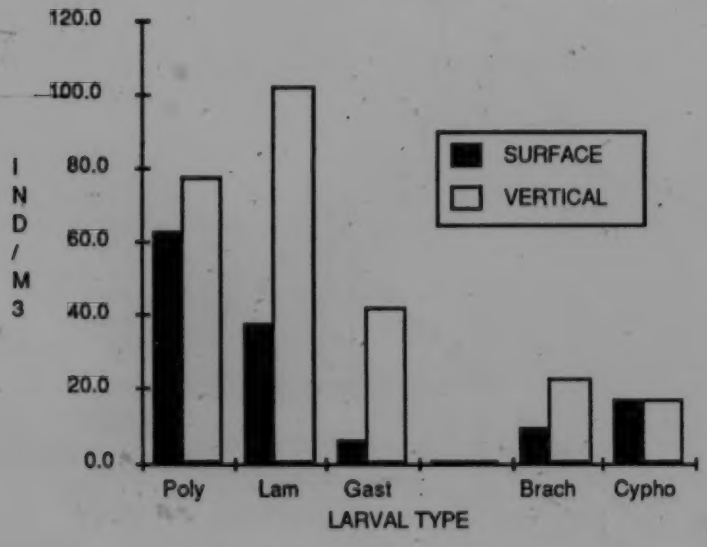


Figure II-21. Abundances of larval types observed in surface and vertical (0-80 m) hauls taken during daytime on 9/11/84. Counts have been standardized to numbers of larvae per m^3. Legend for the abcissa is: Poly, Polychaete trochophores; Lam, Lamellibranch veligers; Gast, Gastropod veligers; Cirrip, Cirripede nauplii; Cypho, Cyphonautes larvae; Ophio, Ophioplutei.

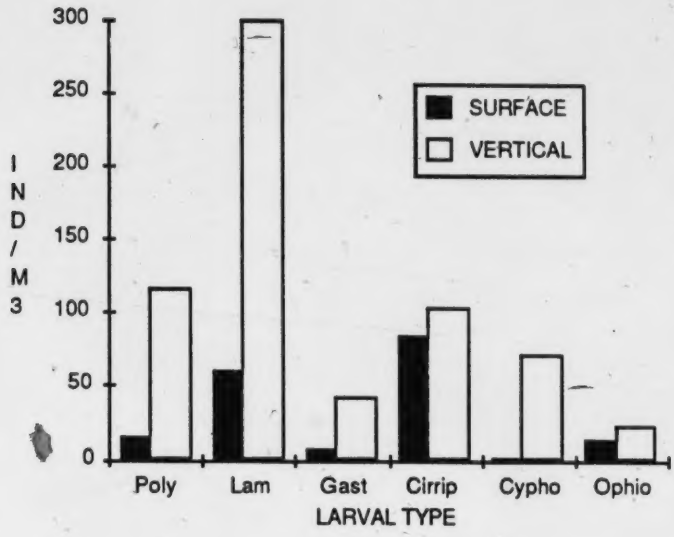

300
250
200
150
100
50
0
IND/M3
SURFACE
VERTICAL
Poly
Lam
Gast
Cirrip
Cypho
Ophio
LARVAL TYPE

Figure II-22. Compilation of the larval types by period of peak abundance, with data from Table II. The histogram shows that the larval fauna was most varied during Feb-Mar and Jun-Jul. The overlay plots are mean semimonthly temperature and plankton data from Figures 2 and 4; wet weights are plotted on a relative scale (see Fig. 4 for absolute values).

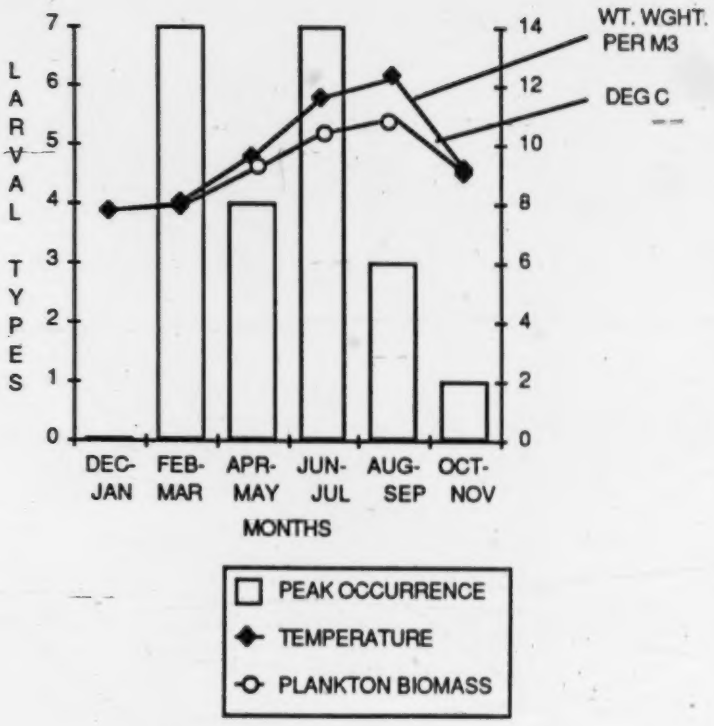
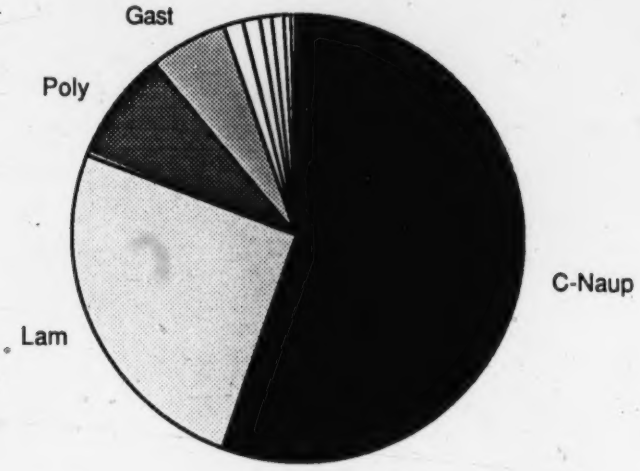
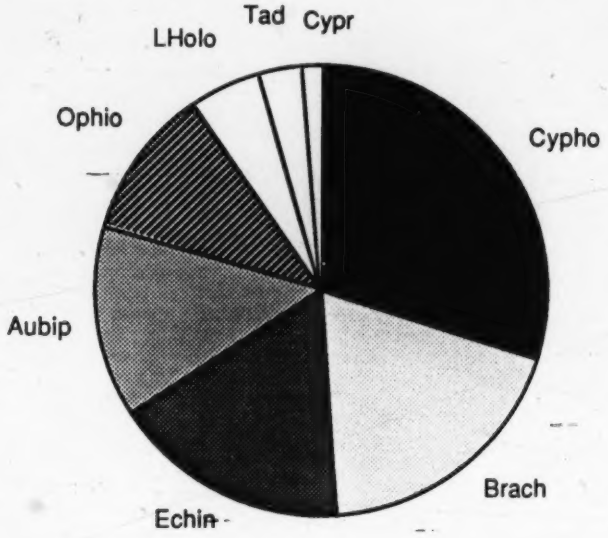

LARVAL TYPES
0
1
2
3
4
5
6
7
0
2
4
6
8
10
12
14
WT. WGHT. PER M3
DEG C
DEC-JAN
FEB-MAR
APR-MAY
JUN-JUL
AUG-SEP
OCT-NOV
MONTHS
PEAK OCCURRENCE
TEMPERATURE
PLANKTON BIOMASS

Figure II-23. Pie charts showing relative abundances of the larval types in all samples combined. In (A) data for all larval types are included, while in (B) data for cirripede nauplii (C-Naup), lamellibranch veligers (Lam), polychaete trochophores (Poly) and gastropod veligers (Gast) have been excluded [pie (B) represents 5% of (A)] to show relative abundances of the less common larval types. Legends for the remaining larval types are: Cypho, cyphonautes larvae; Brach, brachyuran zoeae; Echin, echinoplutei; Aubip, auricularias and bipinnarias; Ophio, ophioplutei; LHolo, lecithotrophic holothurian and asteroid larvae; Tad, ascidian tadpole larvae; Cypr, cirripede cyprid larvae.

A. Relative abundance of all larval types



B. Relative abundance of larval types, common types deleted



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III. STAGE-SPECIFIC PREDATION UPON EMBRYOS AND LARVAE OF THE PACIFIC SAND DOLLAR, DENDRASTER EXCENTRICUS, BY ELEVEN SPECIES OF COMMON ZOOPLANKTONIC PREDATORS

INTRODUCTION

[1] Predation is a major source of mortality for pelagic larvae of benthic marine invertebrates (Thorson, 1946, 1950; Young and Chia, in press). Although planktivores eat invertebrate larvae, most studies of predator / prey interactions in the plankton consider larvae only as incidental prey (reviewed by Young and Chia, in press). Most models of "reproductive strategies" of marine invertebrates assume that rates of predation upon larvae are high and constant during development (Vance, 1973; Jackson and Strathmann, 1981; etc.), though Christiansen and Fenchel (1979) and Pechenik (1979) have suggested that embryos and early larvae might be more susceptible to predation than late-stage larvae. In spite of considerable interest in larval life histories, only Cowden et. al. (1984), Pennington and Chia (1984 [Chapter IV], 1985 [Chapter V]), and Rumrill et al. (1985) have conducted experimental studies which examine aspects of predation upon larvae of benthic invertebrates.

In this study we document patterns of predation by eleven common planktivorous species upon embryonic and larval stages of the Pacific sand dollar, Dendraster excentricus (Eschscholtz), to determine if rates of predation by a variety of predators upon embryos and larvae are constant during development, or if they are stage-dependent and decrease as development proceeds (see Rumrill et al., 1985). Dendraster embryos and larvae were chosen as prey because they were readily available, and because they feed and develop in the plankton for many weeks (Strathmann, 1978) where they are exposed to a variety of predators. The predator species were common in the plankton near Friday Harbor, Washington, where the study was conducted.

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[1]This chapter is in press: Pennington, J.T., S.S. Rumrill and F.S. Chia. Stage-specific predation upon embryos and larvae of the pacific sand dollar, Dendraster excentricus, by eleven species of common zooplanktonic predators. Bull. Mar. Sci.

MATERIALS AND METHODS

Adult Dendraster excentricus were collected from intertidal sand flats on Orcas Island, Washington, and their embryos and larvae were cultured as described by Highsmith (1982). Embryonic and larval development was divided into 7 prey stages: (1) unhatched embryos; (2) blastulae; (3) gastrulae; (4) prism larvae; (5) 4-armed plutei; (6) 6-armed plutei; and (7) 8-armed plutei (see Mortensen, 1921). Predation experiments were conducted separately for each of the first 5 prey stages for all predators and for all 7 stages for one predator; however, because development is continuous and rapid during the 3-4 days following fertilization, some experiments necessarily bridged more than one prey stage (see Figs. 1-2).

Except for juvenile pink salmon, which were hatchery-reared, the predator species (Table I) were collected in the vicinity of Friday Harbor Laboratories. The copepods, euphausids, amphipods and chaetognaths were taken in a 330 um mesh plankton net equipped with a non-filtering cod end. The hydromedusae, ctenophores and zoea larvae were dipped from surface waters in hand-held jars. Sticklebacks were captured with a beach seine. Except for fish, predators were used in experiments on the day of collection. The fish were maintained in flow-through aquaria at ambient seawater temperature and fed goldfish food and chopped shrimp prior to experiments.

For experiments, Dendraster embryos or larvae were counted into a series of jars nearly filled with 3 um-filtered seawater. Predators were then added to treatment jars, but not to control jars which measured background prey mortality. The number of treatment and control replicates varied in some experiments (Figs. 1-2), as did the number and sizes of predators (Table 1). In some cases, experiments with different predator species were run simultaneously (in parallel), so that jars lacking predators served as controls for both experiments. Except for experiments with euphausids and zoeae, prey density was always 50/l, and experiments were conducted in 1 l jars. Experiments with zoeae were also conducted in 1 l jars, but at 3 prey densities, either 25, 50, or 100 prey/l. Experiments with euphausids were conducted in gallon jars each containing 3 l of seawater and 100 prey. The jars were sealed and strapped around the long axis of a grazing wheel (see Landry, 1978; Yen, 1982) which rotated about 1.6 rpm to keep the predators and prey suspended. Experiments ran for 24 hours at 12° C in a coldroom under a 12:12 light:dark

photoregime. At the end of experiments, predators were removed and water was siphoned from the jars through Nitex mesh, concentrating the surviving prey in a small volume of residual seawater. The prey were then washed into vials, fixed, and counted later.

RESULTS

The results of the predation experiments are shown as Figs. 1-2. Statistical analysis was performed with square-root transformed percentages because Bartlett's test indicated this transformation usually rendered the data sufficiently homoskedastic for analysis of variance (ANOVA). However, the data for Pseudocalanus minutus and Euphausia pacifica were not homoskedastic after transformation; though the trends in rate of predation were very strong for these predators (Fig. 1a-b), some caution must nevertheless be used in interpreting these statistical results. Values for control replicates for all prey stages offered to a given predator species (or group of predator species where experiments were run in parallel) were averaged because one-way ANOVA's indicated that loss from control jars was independent of prey stage ($P>.05$). An ANOVA followed by a Student-Newman-Keuls multiple range test was then calculated with the data for each predator species to determine where significant differences between control and treatment means lay ($P<.05$). Degrees of freedom for all statistical tests were based on number of replicate jars used during experiments (not on the numbers of predators added).

Three of the crustaceans, Pseudocalanus, Euphausia and the brachyuran zoeae, exhibited similar patterns of predation upon embryos and larvae of Dendraster excentricus, primarily eating young prey stages (Fig. 1a-b,d). All three species ate unhatched embryos at significantly higher rates than plutei. Hatched embryos were also consumed at high rates by Psuedocalanus, but at an intermediate rate by Euphausia Prism larvae were consumed at an intermediate rate by zoeae, and at a low rate by Euphausia. The amphipod Parathemisto pacifica did not eat large numbers of any prey stage (Fig. 1c), though it ate significantly more gastrulae and prism larvae than other stages. Detailed results of the prey density (functional response) and other experiments with zoeae are presented elsewhere (Rumrill et al., 1985).

The hydromedusae Aequorea victoria and Phialidium gregarium also consumed significantly more early-stage prey than plutei (Fig. 1e-f). Aequorea ate most unhatched embryos and swimming blastulae and gastrulae offered. Phialidium ate most of the immotile embryos, but did not capture motile prey in significant numbers.

The ctenophore Pleurobrachia bachei ate neither embryos nor larvae in significant numbers (Fig. 1g), while Bolinopsis infundibulum may have consumed a few plutei (Fig. 1h).

The fish, Oncorhynchus gorbuscha (pink salmon) and Gasterosteus aculeatus (sticklebacks), consumed relatively few blastulae and gastrulae but ate significant numbers of unhatched embryos, prism and pluteus larvae (Fig. 2a-b).

The chaetognath Sagitta elegans did not consume large numbers of embryos or larvae (Fig. 2c). However, it apparently ate more hatched embryos than immotile embryos or plutei.

DISCUSSION

Ten of the eleven predator species fed during experiments, and for those, rates of predation were never constant for all prey stages. The patterns of predation observed were presumably caused by the behavioral and morphological changes that the prey undergo during development. Unhatched embryos are immotile and surrounded by the fertilization envelope and jelly coat, which in Dendraster excentricus contains pigment cells. Blastulae and gastrulae are motile and have hatched out of the jelly coat and fertilization envelope. Prism larvae are transitional between gastrulae and plutei, and bear some features common to both stages. Plutei are both behaviorly and morphologically more complex than earlier stages. Plutei swim, but also stop, turn or back up when they encounter objects or are disturbed. The arms of plutei are supported by a calcite endoskeleton, which Emlet (1983) has shown is stronger than necessary to simply support the arms during swimming, and plutei also grow from about 225 um long as 4-armed plutei to about I mm long as 8-armed larvae. We have not determined the causes of differential vulnerability to predators (see Rumrill et al., 1985), but it is not surprising that fundamental changes in morphology and behavior produce stage-selective predation.

The predator species used different feeding mechanisms, and they produced different patterns of predation. However, the patterns fall into four general groups which

are discussed below:

(1) Three crustacean species consumed primarily embryo through gastrula stages, but few plutei. The size, motility or larval spicules of plutei apparently protects them from these predators. It is also possible that the crustaceans simply became satiated when offered plutei, though functional response experiments with zoeae indicate this was unlikely (Rumrill et al., 1985). The hydromedusae also fed primarily upon early stages though their method of prey capture is unlike that of crustaceans. Because both medusa species eat prey larger than plutei (Hyman, 1940; Huntley and Hobson, 1978) and the internal skeleton of plutei cannot protect against nematocysts, mobility of plutei may be important in avoiding these predators. However, Aequorea victoria ate significant numbers of all prey stages while Phialidium gregarium ate only unhatched embryos. This result is in general agreement with Hyman's (1940) finding that Aequorea is a relatively indiscriminant planktivore, and with R. Larson's (pers. comm.; Univ. Victoria) observation that Phialidium manubria and guts often contain crustacean eggs.

(2) The amphipods and chaetognaths both ate more blastula through prism stages than unhatched embryos or plutei.

(3) The two fish species consumed both unhatched embryos and plutei, but ate significantly fewer intermediate stages. We observed both fish species striking at plutei in aquaria; the fish clearly saw, and then ate plutei. It is not clear, however, why unhatched embryos were consumed at high rates while blastulae and gastrulae were eaten at the lowest rates. It is possible that jelly coat surrounding unhatched embryos, which in Dendraster contains purple pigment cells, increased their diameter and visibility so that the fish were able to see and eat them. Conversely, some prey mortality may have occurred during gill ventilation.

(4) The ctenophore species ate few, if any prey, though Bolinopsis infundibulum apparently ate a few plutei. Pleurobrachia bachei does eat copepod prey in similar experiments (C. Greene; pers. comm.; Univ. Washington). These ctenophore species probably specialize on faster-swimming crustacean prey, and may not have responded to the immotile or slow-swimming prey in our experiments. Anderson (1974) found that slow-swimming copepods formed a large fraction of the diet of Bolinopsis, while swifter copepods occurred more frequently in the diet of Pleurobrachia. Possibly plutei, but not

earlier stages, are large or motile enough to be captured by Bolinopsis, but not by Pleurobrachia.

The above groupings, based on patterns of predation, with but one exception also sort the predators by taxa. Thus the hydromedusae and three of the four crustacean species comprise group 1, although the amphipod species forms group 2 with the chaetognath species. The fish species comprise group 3, while the ctenophores form group 4. Such a construct is analogous to the "functional group" classification used to describe patterns of predation by collections of planktivores that feed with similar mechanisms (see Greene, 1983, 1985). In such models prey selection by a given predator type is predicted in terms of prey size and swimming speed. Our results indicate that predators with similar feeding mechanisms generally do eat similar prey. However, Greene's (1983; 1985) predictions are not clearly borne out. Though the crustaceans did eat small prey, medusae, ctenophores and chaetognaths did not predominantly eat large prey, as predicted. Similarly, the fish species did eat large plutei, but they also ate unhatched embryos. Based on our results, classification of predators by taxa would seem simpler and as explanatory as the functional group construct.

Of the eleven predator species, the nine invertebrates ate few or no plutei while only the fish consumed more plutei than earlier stages. Because the planktonic abundance and encounter rates of the prey and most of the predators are unknown, we cannot predict mortality rates for embryonic or larval Dendraster in the plankton. The predators and prey were also subjected to unnatural treatment both before and during experiments which probably altered rates of predation for particular predators. Nonetheless, within the constraints of the experimental design, the results do indicate that planktonic rates of predation upon Dendraster embryos and larvae are stage-dependent for a variety of common predator species and that where invertebrate predators predominate, rates of predation upon plutei are lower than upon earlier stages. Conversely, where small planktivorous fish are common, plutei may be consumed at high rates. At present, such complexity of interaction between predators and their larval prey is not reflected in most models of larval life-histories. Christiansen and Fenchel (1979) and Pechenik (1979) have shown that where stage-dependent mortality rates occur, they should affect "reproductive strategies".

The patterns of predation we have documented for Dendraster embryos and larvae may be common for invertebrate larvae from a variety of taxa. Because predation is a major cause of mortality for larvae of benthic invertebrates (Thorson, 1946; 1950; Young and Chia, in press), selective pressure for larval defenses should be substantial and a variety of defenses have probably evolved. It will be of interest to examine such defenses, and to determine whether the interactions of other larvae with their predators will also fall into decipherable patterns.

Table 1. List of planktivorous invertebrates and fish used in predation experiments with embryonic and larval stages of *Dendraster excentricus* as prey. Number of predators used per replicate and approximate predator length or diameter is also noted.

PREDATOR PHYLUM	PREDATOR SPECIES	# PREDATORS PER REPLICATE	PREDATOR SIZE (mm)
ARTHROPODA:	*Pseudocalanus minutus* (Copepoda)	25	1.2
	Euphausia pacifica (Euphausidacea)	2	30
	Parathemisto pacifica (Amphipoda)	5	2-4
	brachyuran zoeae	5	3
CNIDARIA:	*Aequorea victoria*	1	50
	Phialidium gregarium	2	15
CTENOPHORA:	*Pleurobrachia bachei*	1	10
	Bolinopsis infundibulum	1	30
CHAETOGNATHA:	*Sagitta elegans*	5	30
CHORDATA:	*Oncorhynchus gorbuscha* (Pisces)	2	40
	Gasterosteus aculeata (Pisces)	2	55

Figure III-1. Percentages (±1 standard deviation) of embryonic and larval stages surviving experiments with crustacean and coelenterate predators: (A) the copepod Pseudocalanus minutus; (B) the euphausid Euphausia pacifica; (C) the amphipod Parathemisto pacifica; (D) brachyuran zoeae; (E) the hydromedusan Aequroea victoria; (F) the hydromedusan Phialidium gregarium; (G) the ctenophore Pleurobrachia bachei; (H) the ctenophore Bolinopsis infundibulum. Legend for the abscissa: C, controls; E, unhatched embryos; B, blastulae; G, gastrulae; P, prism larvae; 4, 4-armed plutei; 6, 6-armed plutei; 8, 8-armed plutei. The number of replicates of each treatment is noted in the upper right corner of each bar. The letters in or over each bar indicate the results of a Student-Newman-Keuls Multiple Range Test; where the same letter occurs in or over 2 or more bars they were grouped as not significantly different ($P > .05$).

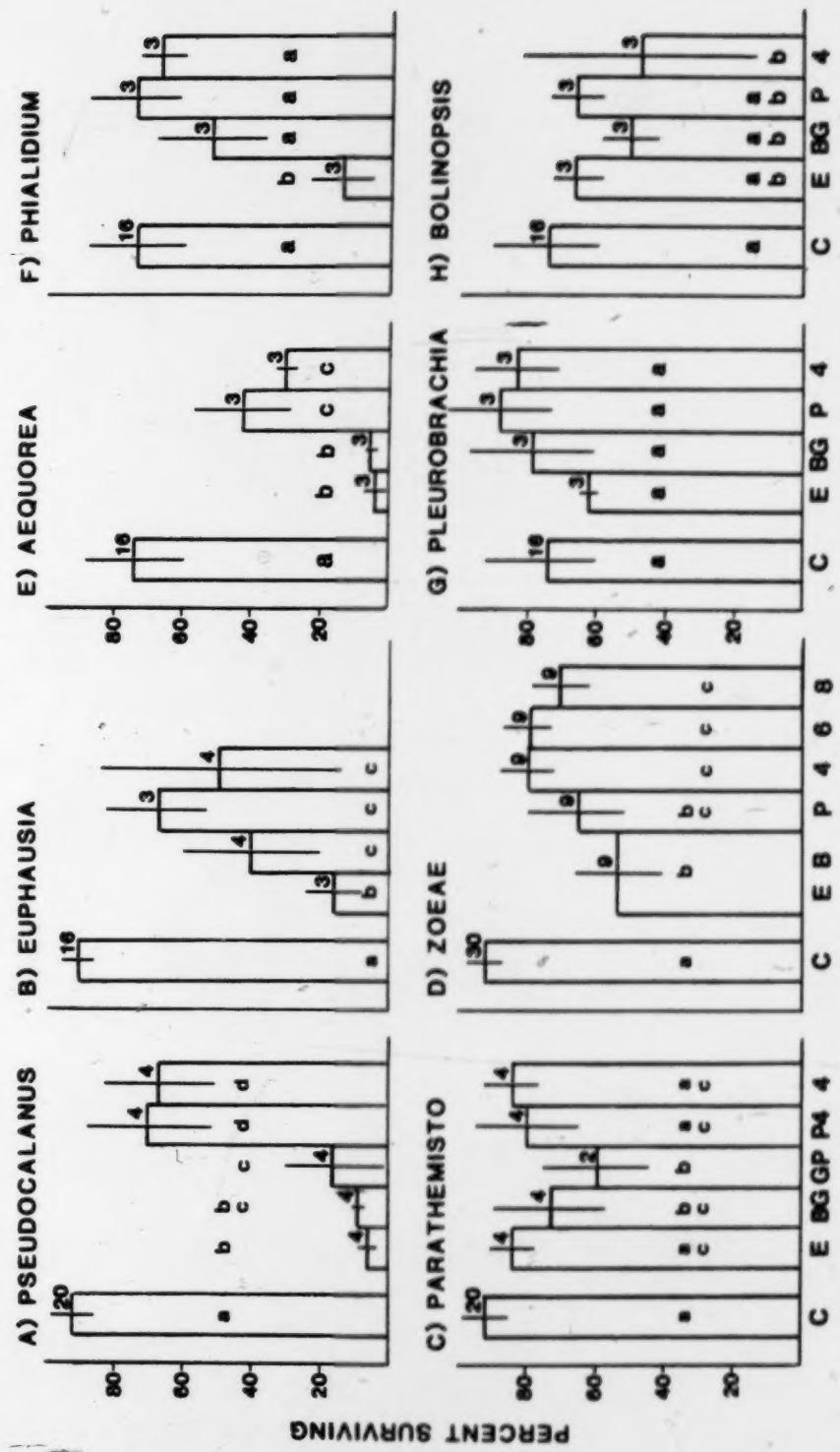
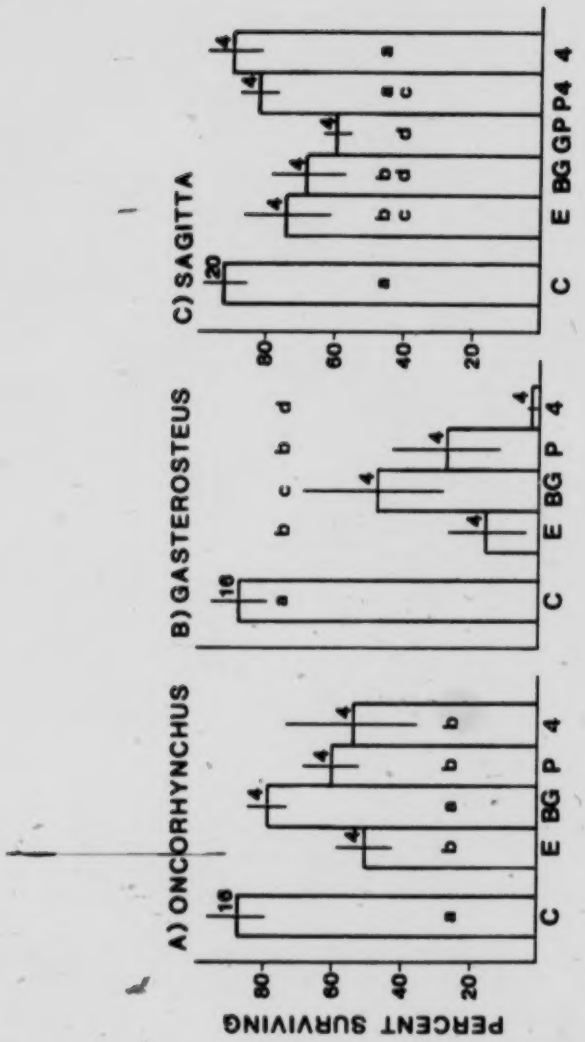

A) PSEUDOCALANUS
B) EUPHAUSIA
E) AEQUOREA
F) PHIALIDIUM
C) PARATHEMISTO
D) ZOEAE
G) PLEUROBRACHIA
H) BOLINOPSIS
PERCENT SURVIVING
C E BG GP P4 4
C E B P 4 6 8
C E BG P 4
C E BG P 4

Figure III-2. Percentages (± 1 standard deviation) of embryonic and larval stages surviving experiments with planktivorous fish and a chaetognath: (A) juvenile pink salmon, Oncorhynchus gorbuscha; (B) sticklebacks, Gasterosteus aculéatus; (C) the chaetognath Sagitta elegans. See caption of Fig. 1 for legend to abscissa and key to statistical results.


PERCENT SURVIVING
A) ONCORHYNCHUS
B) GASTEROSTEUS
C) SAGITTA
C E BG P 4
C E BG P 4
C E BG GP P4 4

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IV. MORPHOLOGICAL AND BEHAVIORAL DEFENSES OF TROCHOPHORE LARVAE OF SABELLARIA CEMENTARIUM (POLYCHAETA) AGAINST FOUR PLANKTONIC PREDATORS

INTRODUCTION

[2] Thorson (1946), Young and Chia (in press), and others have suggested that the major source of larval mortality for benthic marine invertebrates is predation. While this conjecture may be true, little empirical information supports it. Predation upon invertebrate larvae is generally documented during gut content anaylsis of predators; larvae usually constitute a minor portion of the diet (reviewed by Young and Chia, in press), and larvae thus observed are often partially digested and therefore difficult to identify. However, Cowden et al. (1984) provide data on differential predation upon several pelagic larvae by two benthic filter-feeders. Models of reproductive strategies of benthic invertebrates have generally assumed that rates of predation upon larvae are constant throughout ontogeny (Vance, 1973; Pechenik, 1979; Jackson and Strathmann, 1981), though Christiansen and Fenchel (1979) did consider large, late-stage larvae less susceptible to predation than small, early larvae.

Motility is a factor which may alter rates of predation upon developing larvae. Gerritsen and Strickler (1977) have predicted on the basis of encounter rates that prey could minimize predation by minimizing movement. However, it remains unclear whether diversity of planktivores and feeding mechanisms will render this hypothesis relatively unimportant in marine enviornments, especially for slow-swimming invertebrate larvae.

A second factor which may alter rates of larval predation is the development of structures such as larval setae (Fig. 1d). A wide variety of planktonic organisms develop setae or spines, including larvae of many benthic polychaetes (Bhaud and Cazaux, 1982; review by Schroeder and Hermans, 1975) and articulate brachiopods (Long, 1964). These larval setae project posteriorly during normal swimming, but are erected to spread out radially when larvae encounter objects or are otherwise disturbed (Fig. 1b-c). Since larval setae are typically lost during metamorphosis, they are presumed to be adaptations for

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[2]This chapter has been published: Pennington, J.T. and F.S. Chia. 1984. Morphological and behavioral defenses of trochophore larvae of Sabellaria cementarium against four planktonic predators. Biol. Bull. 167: 168-185.

pelagic existence. Setae and spines have been postulated to function both as "parachutes" which slow sinking rates and as defense mechanisms (Wilson, 1929, 1932; Hardy, 1956; Blake, 1969; Fauchald, 1974; Schroeder and Hermans, 1975). In defense, setae are presumed to function both by increasing a larva's effective size and by making it difficult to swallow. Spines of freshwater rotifers and cladocerans are known to be effective defenses against small planktivorous invertebrates, but are apparently not effective defenses against fish predation (Gilbert, 1966; Dodson, 1974; Kerfoot, 1975, 1978, 1980). The only observations regarding the function of setae or spines for marine organisms are those of Lebour (1919) and Wilson (1929). Lebour (1919) observed a megalopa's dorsal spine lodging the larva into the esophagus of a small fish; the fish was neither able to expel or ingest it and eventually died. Wilson (1929) described small fish ejecting Sabellaria alveolata trochophores from their mouths and suggested that erected setae rendered the trochophores offensive.

This study was designed to examine whether motility and setae of trochophores of the polychaete Sabellaria cementarium Moore are effective defenses against predation by four planktonic predators. S. cementarium was used as prey because its embryos and larvae were readily available, and because of the prominent setae that its trochophores develop (Fig. 1b-d).

MATERIALS AND METHODS

Adult Sabellaria cementarium were dredged in the vicinity of San Juan Island, Washington. Gametes were obtained and embryos and larvae were cultured as in Smith (1981). Non-motile eggs, 2 day-old pre-setal trochophores and 5 day-old setose trochophores were used as prey (Fig. 1a-c). Body size and shape was relatively constant during the first five days of development (70-90 um), though eggs were disk-shaped and somewhat broader when freshly spawned.

Predator species from four phyla, Pleurobrachia bachei (Ctenophora), a medusa Aequorea victoria (Hydrozoa), unidentified brachyuran megalopa (Crustacea), and juvenile Sebastes sp. (Pisces), were chosen because they were common near Friday Harbor during summertime, and because of their different feeding mechanisms. Although in some cases predators were kept in the laboratory for several days before experiments and fed

Artemia salina nauplii or goldfish food, they appeared to be in good condition at the time of experiments.

For each experiment fifty eggs or larvae were placed into each of 16 1.0 l jars which contained 960 ml of 3 um filtered sea water. Twelve of the jars were divided into four sets of three replicates. Each set received a different predator species: (1) one 10 mm diameter P. bachei per jar; (2) one 30 mm diameter A. victoria per jar; (3) five 3 mm long megalopa per jar; or (4) two 15 mm long Sebastes sp. per jar. The four remaining jars served as controls, measuring background mortality and handling errors.

All jars were capped and strapped horizontally around the horizontal axis of a "grazing wheel" which rotated at 1.6 rpm, gently stirring the water and keeping the prey evenly distributed within the jars. Experiments were run for 24 hours in a 12:12 light:dark, 14° C coldroom. At the end of each experiment, predators were removed and the water was siphoned from the jars through 41 um Nitex mesh, concentrating the remaining prey in a small volume of residual water. The prey were then washed into vials and preserved in 2% formalin. The preserved prey were later counted in a Bogorov Tray under a dissecting microscope.

Data analysis was performed according to the methods of Zar (1974).

RESULTS

Predation rate upon the three developmental stages of Sabellaria cementarium by each of the four predators is presented in Figures 2a-d. All control values were averaged because loss from control jars was stage-independent; the slope of a least-squares regression of number of larvae missing from controls upon prey stage did not differ significantly from zero (F-test; $P>.05$). A one-way analysis of variance (ANOVA) was calculated from the data for each predator species to determine if there were significant differences between the number of prey missing in the four treatments (controls, eggs, pre-setal trochophores, and setose trochophores). The analyses were done with untransformed data since Bartlett's Test indicated that the data were sufficiently homoskedastic for ANOVA. For all ANOVA's there were significant overall differences between treatments ($P<.02$ or less), indicating that all predators ate some prey. A posteriori Student-Newman-Keuls Range Tests (SNK Tests) were then calculated which

compared all possible combinations of treatments and grouped treatment subsets that were not significantly different ($P<.05$). Because the SNK Test often produces ambiguous results (overlapping non-significant subsets) that are difficult to interpret, a series of *a priori* t-tests were also calculated to determine if particular treatment subsets were statistically significant. Our *a priori* hypothesis was that rate of predation should decline through development. Those statistical ambiguities which remain (below) could probably have been eliminated if more replicates were used.

The different predator species exhibited different rates and patterns of predation upon eggs and pre-setal trochophores, but in all cases setose trochophores were eaten at low rates, not significantly different than control values (Fig. 2; SNK and t-tests, $P<0.01$ or less). For *Pleurobrachia bachei*, the SNK Test grouped values for the controls and setose trochophores as not different or homogeneous, indicating non-significant predation upon setose trochophores. T-tests indicated rate of predation on eggs was significantly higher than that on setose trochophores ($P<0.029$), with rate of predation on pre-setal trochophores lying at an intermediate, non-significantly different value.

For *Aequorea victoria* the SNK Test grouped values for the controls, eggs, and setose trochophores as homogeneous, indicating uniformly low rates of loss from these groups. T-tests indicated the difference in rate of predation between pre-setal and setose trochophores was marginally significant ($P<0.07$). Pre-setal trochophores appear to be more vulnerable to *A. victoria* than eggs and setose trochophores.

The SNK Test indicated that brachyuran megalopa ate significantly more eggs than the other prey stages. T-tests found found that eggs were eaten significantly more often than pre-setal ($P<0.014$) or setose trochophores ($P<0.001$), and that pre-setal trochophores were eaten more often than setose trochophores with marginal significance ($P<0.051$).

For juvenile *Sebastes* the SNK Test again grouped the controls and setose trochophores as homogeneous, indicating non-significant predation on setose trochophores. T-tests indicated that eggs were eaten at somewhat higher rates than setose trochophores ($P<0.074$), with rate of predation on pre-setal trochophores lying at an intermediate value.

DISCUSSION

The effect of prey motility on predation rate varied among predators, probably a result of the predators' different feeding mechanisms. Predation by medusae involves responses to individual prey in the sense that nematocyts must be stimulated to fire, and prey motion is an important cue in this response (Pantin, 1942). Non-motility may explain the lack of consumption of eggs by Aequorea victoria. Prey motion is presumably an important cue for ctenophores and fishes as well, since colloblasts must be stimulated to release adhesive substance in ctenophores (Franc, 1978) and most fish locate prey visually (Kislalioglu and Gibson, 1976; Hyatt, 1979). However, Pleurobrachia bachei and Sebastes sp. did not eat more motile than nonmotile prey.

Megalopa ate significantly more eggs than all other stages of prey. It thus appears that swimming helped trochophores to escape or avoid these predators. The mechanisms by which most megalopa feed on small prey are not known, but many crustaceans both filter small particles and feed raptorially upon larger prey (Marshall and Orr, 1960; McLaughlin, 1982). If the megalopa did filter-feed, prey capture was probably not dependent upon recognition of individual eggs or trochophores. If so, non-motile eggs would be encountered and captured nearly as often as swimming trochophores, but if swimming enabled some trochophores to escape, the rate of predation upon eggs would be higher, as was observed. Swimming may also have reduced rates of predation by P. bachei and Sebastes sp. on both pre-setal and setose trochophores.

Predation upon setose trochophores was insignificant while oocytes and pre-setal trochophores were eaten more often by all predators (except A. victoria, which did not eat eggs). The methods by which setae function defensively have not been investigated, but the radial display of setae could create at least three potential defenses: (1) the effective size of a larva increases; (2) a buffer zone of setae and water around a larva's tissue is formed; (3) the barbed setae become oriented so that they may pierce objects impinging upon a larva. The possible roles of these mechanisms are discussed below.

Erection of setae increases the overall diameter of a larva, possibly deterring predation by small-mouthed predators as has been shown for freshwater rotifers (Gilbert, 1966). However, the predators used in the present experiments all eat prey much larger, in all dimensions, than trochophores. Reeve et al. (1978) fed Pseudocalanus minutus (<650

um long) to P. bachei during production experiments, and Lebour (1924) observed P. bachei eating larval fish. A. victoria has been commonly observed eating large prey, including fish and other jellyfish (Lebour, 1924; Hyman, 1940; Arai and Jacobs, 1980). The juvenile Sebastes sp. fed successfully on Artemia salina nauplii (ca 600 um) as well as upon pieces (<1 mm) of goldfish food. Many species of crab larvae are also cultured successfully on A. salina (Rice and Williamson, 1971), and the megalopa used in these experiments fed on goldfish food as well. It thus seems unlikely that the size increase created by setal erection prevents predation by any of the predator species used here. However, megalopa have far smaller mouths than the other predators tested; erected setae may substantially increase handling difficulty if megalopa cannot swallow larvae whole but must manipulate and dismember them. Similarly, spines of cyclomorphic cladocerans and rotifers have been shown to reduce predation by freshwater predators with small mouths (reviewed by Zaret, 1980). It thus seems probable that setae function defensively against small-mouthed predators such as megalopa by increasing handling time. In contrast, the other predator species used here could easily swallow whole setose S cementarium trochophores.

The buffer zone of sea water surrounding a trochophore with erected setae may be important as a defense against medusae and tentaculate ctenophores. As described above, both P. bachei and A. victoria must sense and capture individual prey. If a predator's tentacles touch only the erected setae of a trochophore, the tactile or chemical cues necessary to elicit a response may not be perceived. Further, even if a larva is recognized as food, nematocysts and colloblasts may not work efficiently upon setae or across the buffer zone (ca. 150 um) of water created by the setae. If trochophores are first trapped by nematocysts or colloblasts, then ingested and finally expelled, their chances of surviving are probably slim. The numerous trochophores surviving experiments appeared to be in good shape; few were deformed or entangled in mucus. It seems unlikely that the surviving trochophores were captured at all by these predators, but that setae prevented recognition or prey capture.

Setae may also deter predation by irritating mouthparts as originally implied by Wilson (1929), whose suggestion seems intuitively reasonable because fish capture prey within the buccal cavity where setae could easily pierce oral tissues as trochophores are bitten or swallowed. Predatory fish are also deterred by the spines of sticklebacks

(Hoogland et al., 1957), but the spines of some cyclomorphic rotifers and cladocerans are not considered to be effective against fish (Greene, 1983).

Other work on predation upon marine larvae has found patterns of predation comparable to those presented here. For a predator who senses individual prey at a distance, Landry (1978) found that weakly motile early copepod nauplii were poorly detected by the copepod Labidocera trispinosa, and were thus eaten at low rates. Large active nauplii were eaten at the highest rates, while copepodids developed an escape response and were eaten rarely. Also, work with marine fish larvae as prey for various crustaceans has generally found the non-motile eggs are not detected by predators and are rarely eaten while motile yolk-sac larvae are eaten at high rates. Feeding larvae develop an escape response and are captured and eaten much less often (Lillielund and Lasker, 1971, Theilaker and Lasker, 1974; Bailey and Yen, 1983). The low rates of predation upon later stages in all cases are due to the development of fundamentally new structures or behaviors during ontogeny, processes not observed for freshwater prey (Greene, 1983).

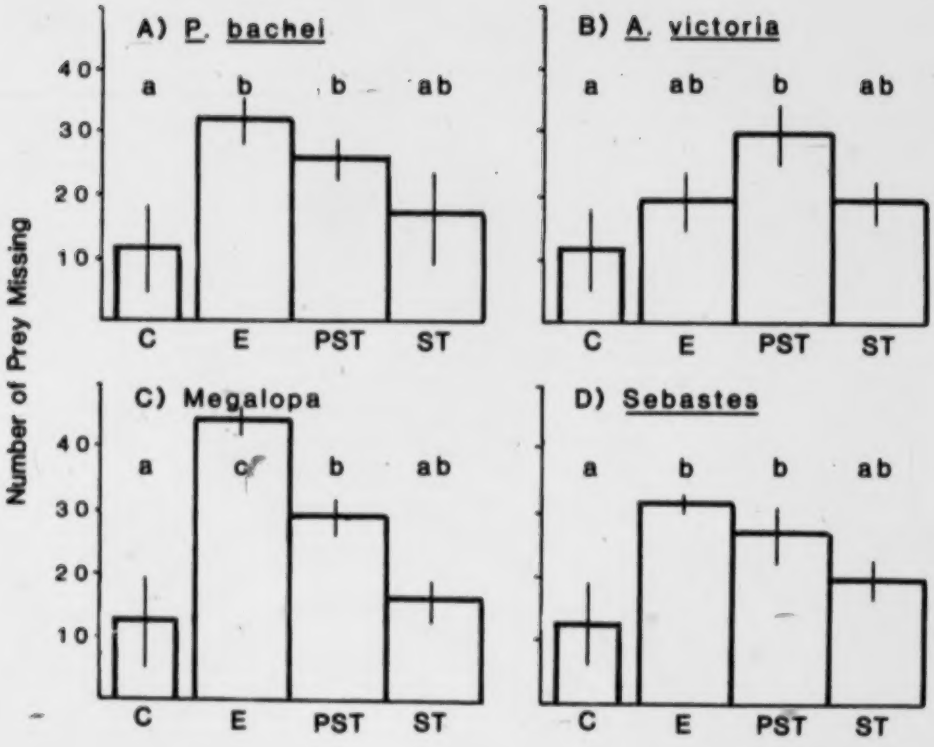
At present it is not possible to assess the potential impact these predators have on pelagic larval populations of S. cementarium. No quantitative estimates of the densities of any of the predator or prey species have been made in the Puget Sound area, though all are common in the plankton during summer. Similarily, except for P. bachei (see Reeve and Walter, 1978), quantitative observations of the predation rates of the predators upon other prey types have not been made. However, for the predators used, we have shown that rates of predation upon setose trochophores are low.

Susceptibility to predation is a ubiquitous and important problem for embryos and larvae of benthic invertebrates (Thorson, 1946; Young and Chia, in press) which should generate strong selective pressures for larval defense. If effective defenses have evolved, larval forms, behaviors, chemicals, and ultimately reproductive strategies should reflect such selection. Reproduction in many benthic invertebrates with pelagic larvae is characterized by a short period of rapid embryogenesis followed by a prolonged period of larval feeding and growth. This pattern may be facilitated by the development of efficient larval defenses.

Figure IV-1. Selected developmental stages of Sabellaria cementarium; A, B, and C slightly compressed and to same scale. A: unhatched embryo of the same size and shape as eggs and pre-setal trochophores; B: five day-old setose trochophore swimming with unerected setae; C: five day-old trochophore with erected setae; D: seta of S. cementarium trochophore. PT, prototroch; PS, provisional setae.

A
B
C
D

Figure IV-2. Histograms showing mean number of Sabellaria cementarium eggs and larvae missing from treatments for each of the four predator species, ± 1 standard deviation. Treatments are C, controls (n=12); E, eggs (n=3); PST, pre-setal trochophores (n=3); ST, setose trochophores (n=3). Letters over each bar denote the results of a Student-Newman-Keuls Multiple Range Test; where the same letter occurs over two or more bars they were grouped as not significantly different ($P<>.05$).


A) P. bachei
a
b
b
ab
B) A. victoria
a
ab
b
ab
C) Megalopa
a
c
b
ab
D) Sebastes
a
b
b
ab
Number of Prey Missing
40
30
20
10
C
E
PST
ST

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V. GASTROPOD TORSION: A TEST OF GARSTANG'S HYPOTHESIS

INTRODUCTION

[3] Gastropod torsion is a morphogenic event which occurs during larval life, and results in a 180° rotation of the shell and viscera relative to the head and foot of the veliger. Many authors have speculated about the adaptive value of torsion (Morton, 1958a), but the hypothesis proposed by Garstang (1928, 1929) remains the most widely accepted (Lever, 1979). Because torsion enables a veliger to retract its head and foot into the shell and subsequently seal the aperture with the operculum, Garstang (1928, 1929) suggested that torsion evolved as a larval defense. Garstang (1929) and several others (Yonge, 1947, 1960; Knight and Yochelson, 1958; Morton, 1958a, b; Fretter and Graham, 1962; Morton and Yonge, 1964; Purcheon, 1968; Yonge and Thompson, 1976) have proposed that torsion arose functionally complete through a single mutation. This view remains tenable because no partially torted fossil gastropods have been found (Knight, 1952; Ghiselin, 1966; Lever, 1979), and retains popularity, in part, because of recent criticism of evolutionary "gradualism" (cf. Eldredge and Gould, 1972). The defensive benefits to this torted larva were apparently great enough that it survived to become the progenitor of the Gastropoda. However, Thompson (1967) criticized Garstang's (1929) hypothesis on the grounds that the head and velum are not clearly more vulnerable to attack than the foot, and that opisthobranch veligers do not require torsion to retract completely within their shells (Thompson, 1958, 1967). Jagersten (1972) also suggested that larvae are usually swallowed whole by their predators, and the ability to retract the head first is probably more important to adults than to larvae.

Because the torted condition persists in most juvenile and adult gastropods, Garstang (1928, 1929) further suggested that torsion in larvae may create maladaptive features for adults. It has been suggested that shell slits, pallial asymmetries and detorsion in opisthobranch gastropods have evolved, at least in part, to correct detrimental features of torsion for benthic existence (Garstang, 1929; Borradaile et al., 1951; Yonge, 1960). Conversely, Garstang's (1929) hypothesis has been modified because it does not postulate advantages for benthic gastropods. Alterations of mantle position or shell size,

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weight, coiling, or position have all been suggested to be advantageous consequences of torsion for benthic gastropods (Lang, 1900; Naef, 1911; Yonge, 1947, 1960; Borradaile et al., 1951; Morton, 1958a, b; Allen, 1963; Morton and Yonge, 1964; Ghiselin, 1966; Purcheon, 1968; Jagersten, 1972; Underwood, 1972; Solem, 1974; Lever, 1979; Stanley, 1982). To date, no experimental data have been produced to test Garstang's (1928, 1929) hypothesis, or any other proposed function of gastropod torsion.

This study was designed to test Garstang's (1928, 1929) hypothesis by comparing mortality rates of pre-torsional and torted veligers of the abalone Haliotis kamtschatkana Jonas, when offered as prey to an array of seven planktonic predator species from four phyla. The development of H. kamtschatkana has been briefly described by Caldwell (1981), and is similar to that reported for other haliotids (Crofts, 1938; Ino, 1953; Carlisle, 1962; Leighton, 1972, 1974). The pre-torsional and torted veligers used in experiments were nearly identical in size and swimming ability, though the torted veligers had undergone only the first 90° of torsion (see Crofts, 1938). At this stage, torted veligers were fully capable of retracting and sealing the shell aperture with the operculum; the pre-torsional veligers could also retract but had not yet developed an operculum.

MATERIALS AND METHODS

Gametes were obtained according to the methods of Morse et al. (1977, 1978), and embryos and larvae were cultured about 48 hrs (pre-torsional veligers) or 120 hrs (torted veligers) at 8-10° C in 3 um filtered seawater plus 50 ug/l each of penicillin G and streptomycin sulphate. Predators were hand-dipped from surface waters near Friday Harbor Laboratories and used in experiments on the day of collection, or fed and maintained a few days in running seawater prior to experiments.

The experiments were similar to those of Pennington and Chia (1984 [Chapter IV]) and Rumrill et al. (in press), which documented stage-specific predation upon other larval types. Two experiments were conducted. In the first, pre-torsional veligers were used as prey, and in the second, torted veligers were used. For each experiment 50 veligers were placed into each of 40 one-liter jars containing filtered seawater. Thirty-five of the jars were divided into seven sets of five replicates. Each jar within a set then received a predator species as follows:

(1) five brachyuran megalopa larvae (Decapoda);

(2) five Epilabidocera longipedata (Copepoda);

(3) one 30 mm diameter Aequorea victoria (hydromedusa);

(4) one 12 mm diameter Phialidium gregarium (hydromedusa);

(5) one 10 mm diameter Pleurobrachia bachei (Ctenophora);

(6) one 20 mm long Bolinopsis infundibulum (Ctenophora); or

(7) two 30 mm long Oncorhynchus gorbuscha (Pisces).

No predators were added to the five remaining jars which served as controls to measure background prey mortality and handling errors.

During experiments, jars were strapped around the horizontal axis of a grazing wheel (see Landry, 1978; Yen, 1982), which gently stirred the water to keep the prey evenly distributed. Experiments were run for 15 h in a 8:7 h light:dark, 9° C coldroom. At the end of experiments, predators were removed and prey were concentrated by siphoning most of the water off through Nitex mesh. Surviving prey were fixed, and counted later. A one-way analysis of variance and a Student-Newman-Keuls range test was calculated with log-transformed data (not values for "Net Predation", see Fig. 1) for each predator species. These statistics tested for significant differences between control values and values for treatments with predators, and also for differences in rate of predation upon pre-torsional and torted veligers.

RESULTS

Results of the experiments (Fig. 1) show that with the exception of Pleurobrachia bachei ($P>.05$), all predators ate significant numbers of veligers ($P<.007$). P. bachei apparently did not consume veligers, though it does eat other planktonic prey in similar experiments (Pennington and Chia, 1984 [Chapter IV]). Rates of predation upon pre-torsional or torted veligers were significantly different only for the megalopa and Aequorea victoria ($P<.05$). The megalopa consumed more torted veligers while A. victoria ate more pre-torsional veligers.

DISCUSSION

Except for Aequorea victoria, no predator species ate significantly fewer torted than pre-torsional veligers. Moreover, any advantage torsion confers to veligers against predators such as A. victoria is apparently offset by increased vulnerability to predators such as megalopa, and the apparent effectiveness of torsion against A. victoria is not general for hydromedusae, because Phialidium gregarium ate nearly equal numbers of both stages of prey. Our results thus do not support Garstang's (1928, 1929) hypothesis concerning the defensive value of torsion in veligers.

We have not determined why torted veligers, which have developed an operculum and can seal themselves within their shells, were as vulnerable to predation as pre-torsional veligers. Shells of larval molluscs have often been suggested to serve defensively, and several authors have even suggested that veligers can pass unharmed through the guts of their predators (Morton and Yonge, 1964; Yonge and Thompson, 1976; others reviewed by Mileikovsky, 1974). Torted veligers placed on a glass slide usually withdrew upon being disturbed for only a few seconds; perhaps this intermittent retraction was insufficient to deter predators that swallow prey whole. Empty veliger shells were often found within the manubria of P. gregarium at the end of experiments. Shell fragments were also commonly found within jars that had contained crustacean predators. If the crustacean predators broke shells prior to ingestion, retraction probably did not protect the larva within. Mileikovsky (1974) suggested that if veligers do pass intact through the guts of their predators, they are usually so entangled in mucus and feces that they rarely survive.

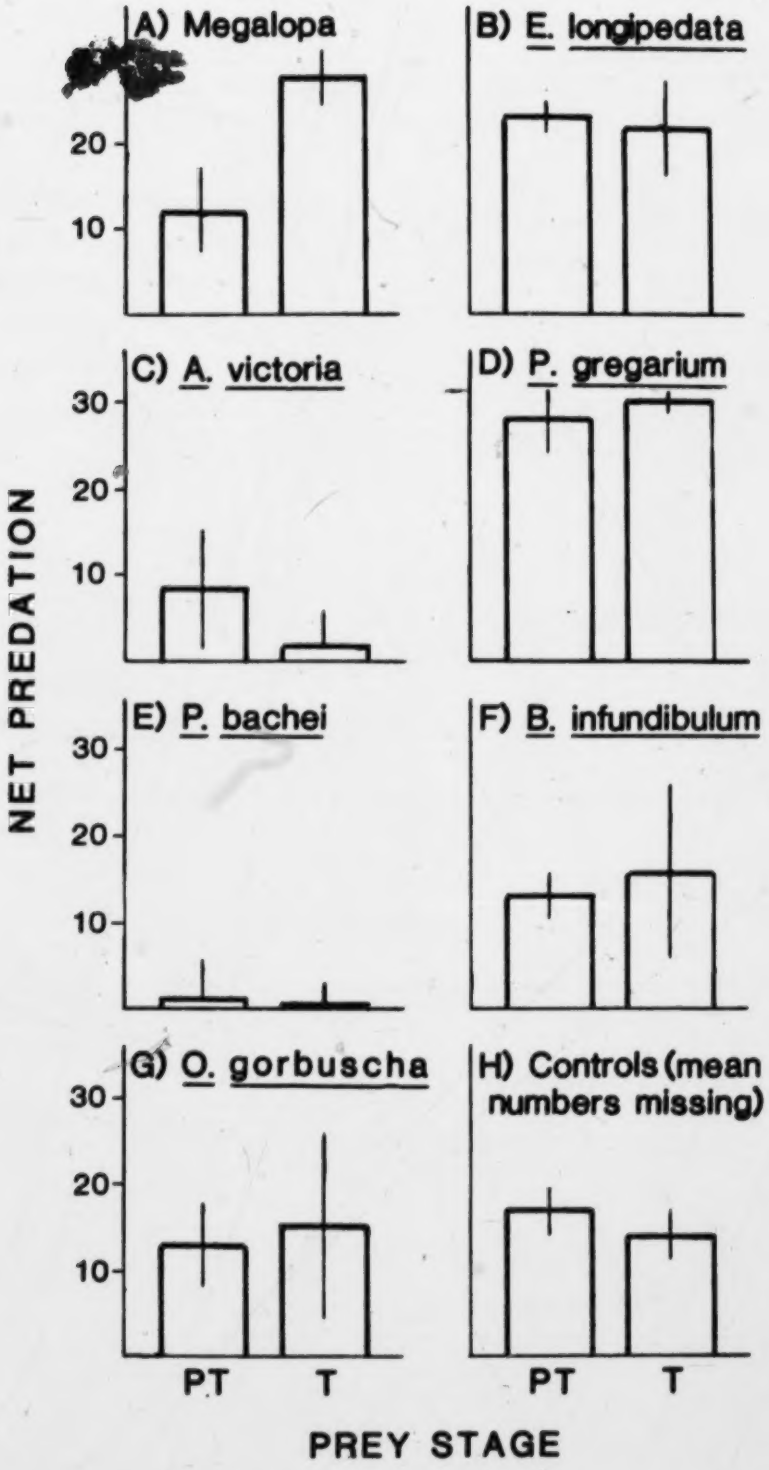
The present study provides the first data to test any hypothesis concerning the adaptive value of gastropod torsion. It might be argued that over evolutionary time, small (and therefore undetected by us) decreases in rate of predation due to torsion would provide sufficient selective pressure to maintain the trait. While this argument is valid, Garstang (1928, 1929) and several recent authors (Yonge, 1947; Knight, 1952; Knight and Yochelson, 1958; Morton, 1958a, b; Morton and Yonge, 1964; Purcheon, 1968; Yonge and Thompson, 1976; Stanley, 1982) have proposed that a single mutation caused torsion in a larval pre-gastropod whose fitness became so enhanced that it became the progenitor of the Gastropoda. Our results indicate that the defensive benefits of torsion for veligers,

if any, are probably insufficient to foster the foundation of the Gastropoda from a mutation in a single veliger. Our results do support the suggestions of Thompson (1967) and Jagersten (1972), both of whom thought that torsion does not function effectively as a larval defence. It nevertheless remains conceivable that torsion confers other benefits to veligers; for example, torsion might aid in swimming (Underwood, 1972), and it is also possible that torsion protects veligers from adverse physical conditions. Pre-torsional veligers do retract within their shells, though they lack opercula.

It is also possible that untested or extinct predators are deterred by torsion while the predators we used are not. Although our selection of predator species was necessarily limited, we attempted to choose a diverse array of predators that are both common in neritic plankton and which feed by different mechanisms (see Pennington and Chia, 1984 [Chapter IV]). Ctenophores, medusae, crustaceans, and planktivorous fish meet these criteria, though it remains problematic whether a predator such as O. gorbuscha had analogues in Cambrian seas. Though we cannot eliminate the possibility that extinct predators provided the selective pressure for torsion in veligers, there is little factual basis to support such an argument.

In contrast to Garstang's (1928, 1929) hypothesis, most other hypotheses regarding torsion postulate advantages during metamorphosis or for juveniles and adults (Lang, 1900; Naef, 1911; Yonge, 1947, 1960; Borradaile et al., 1951; Morton, 1958, 1979; Allen, 1963; Morton and Yonge, 1964; Ghiselin, 1966; Purcheon, 1968; Jagersten, 1972; Underwood, 1972; Solen, 1974; Lever, 1979). If torsion is not a larval adaptation, one or a combination of these hypotheses probably explains its evolution within the Gastropoda. However, the selective pressures that have been suggested to favor torsion will remain conjectural until experimental work is conducted to examine the functional implications of torsion for benthic gastropods.

Figure V-1. "Net predation" upon both pre-torsional (PT) and torted (T) veligers of the archeogastropod Haliotis kamtschatkana Jonas by 7 species of planktonic predators (A-G; see text for complete descriptions of predators). Bars indicate means ± 1 standard deviation. "Net predation" was calculated by subtracting the mean numbers of veligers missing from control treatments without predators (H) from the mean numbers of veligers missing from the treatments with predators. Statistics were calculated with log-transformed raw data; "net predation" was produced for graphic clarity alone. Except for P. bachei (E; $P>.05$), all predators ate significant numbers of prey (analysis of variance; $P<.007$ or less). However, only the megalopa (A) and A. victoria (C) ate significantly different numbers of either pre-torsional or torted veligers (Student-Newman-Keuls range test; $P<.05$).


A) Megalopa
B) E. longipedata
C) A. victoria
D) P. gregarium
E) P. bachei
F) B. infundibulum
G) O. gorbuscha
H) Controls (mean numbers missing)
NET PREDATION
30
20
10
PT
T
PREY STAGE

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VI. PATTERNS OF INTERSPECIFIC AND INTRASPECIFIC PREDATION BY HYDROMEDUSAE ON HYDROZOAN EGGS AND PLANULA LARVAE (*AEQUOREA VICTORIA* AND *PHIALIDIUM GREGARIUM*)

INTRODUCTION

In recent years planktonic cnidarians have been subject to substantial study concerning their population dynamics (Moller, 1980a; Mills, 1981a; Arai and Mason, 1982; Hernroth and Grondahl, 1983; Larson, 1985) and impact on prey communities (McCormick, 1969; Huntley and Hobson, 1978; Moller, 1980b; Purcell, 1981a; Larson, 1985). Organismal features of some species have also been examined; diel vertical migrations have been studied (Moreira, 1973; Yasuda, 1973; Mackie *et al.*, 1981; Arai and Mason, 1982; Mills, 1983, Arkett, 1984, 1985) and the behaviors of a variety of medusae and siphonophores have been observed in large aquaria, by SCUBA divers and from submarines (Hamner *et al.*, 1975; Mills, 1983; Mackie and Mills, 1983). In aggregate these studies have revealed that planktonic cnidarians can regulate abundance of prey species and are an abundant but often-overlooked component of zooplankton communities.

However, relatively little attention has been paid to mechanisms of prey selection by cnidarian zooplankton. The finding that "food juices" and mechanical stimulation in combination cause nematocyst discharge (Pantin, 1942) has not been greatly advanced (see Haynes, 1973; Marsical, 1974; Lenhoff and Lindstedt, 1974) despite an enormous amount of work on the glutathione "feeding response" in *Hydra* (reviewed by Lenhoff, 1974). For example Greene (1985) has categorized zooplanktivores on the basis of their feeding mechanisms ("functional groups"; i.e., medusae as "ambush entangling invertebrates", etc.) and predicted selection of prey on the basis of their size and swimming speed in accordance with the encounter rate model of Gerritsen and Strickler (1977). While such categorization is probably of value (but see Chapter III), the mechanisms underlying observations such as those of Anderson (1974) and Purcell (1981b, 1981c), who reported that some ctenophore and siphonophore species caught larger or faster-swimming prey than others, have not been further resolved.

In constrast, the nematocyst-mediated activities of benthic cnidarians are known to show remarkable sensory discrimination (reviewed by Bigger, 1980; Buss et al., 1984). Not only do nematocysts discharge to secure and paralyse prey, but they are the basis of aggressive interactions between polyps. In anthozoans, nematocysts discharge upon contact with some xenogeneic (heterospecific) polyps and most or all allogeneic (non-clonemate conspecific) polyps, damaging the recipient, but not upon contact with isogeneic (clonemate) polyps (Francis, 1973; Lang, 1973; Potts, 1976; Bigger, 1976, 1980; Lubbock, 1980; Hikada, 1985). Similar interactions have been observed among all conspecific hydrozoan colonies examined to date (Chiba and Kato, 1966; Theodor, 1966; Kato et al., 1967; Ivker, 1972; Tardent and Buhrer, 1982; McFadden et al., 1984; reviewed by Buss et al., 1984). In both anthozoans and hydrozoans special tentacles, polyps, or stolonal growths may be involved in aggressive interactions, but in all cases nematocysts appear to be the primary effectors (see Bigger, 1980; Buss et al., 1984). One or more nematocyst types may be especially abundant on aggressive polyps or stolons (reviewed by Buss et al., 1984), but these types are not apparently restricted to aggressive structures. Similarly, nematocysts on aggressive structures discharge specifically in response to allogeneic or xenogeneic tissues, while at least in some anthozoans, nematocysts on feeding tentacles discharge in response to a wider variety of stimuli which include allogeneic and xenogeneic tissues (Lubbock, 1980). Beyond these generalizations the functional specificities of the numerous nematocyst types, particularly in the Hydrozoa, have been rarely studied (reviewed by Mariscal, 1974). All the above work has indicated a strong genetic determinism in "self-nonself" recognition (Ivker, 1967, 1972; Francis, 1973; Bigger, 1980; Lubbock, 1980; Buss et al., 1984; McFadden et al., 1984).

The leptomedusae Aequoria victoria (Murbach and Shearer) and Phialidium gregarium (A. Agassiz) are the two commonest shallow-water hydromedusae in the San Juan Archipelago, NE Pacific (Mills, 1981a; pers. obs.). During spring and summer both species commonly occur in "swarms" which may cover large areas and last for days (Roosen-Runge, 1970; Arai and Brinckmann-Voss, 1980; Mills, 1981a), and reach peak densities of 5-25 per m^2 at the water surface (pers. obs.). Additionally, swarms of these species often co-occur so that interactions between individuals of the two species are

frequent; medusae of P. gregarium are commonly eaten by A. victoria (Arai, 1980; Arai and Jacobs, 1980). Although Hyman (1940) apparently did not observe A. victoria to eat other hydromedusae, she reported A. victoria to be a "relatively indiscriminant" consumer of other prey types. P. gregarium preys largely on euphausiid eggs and small zooplankton (McCormick, 1969; Larson, 1985).

Because interaction between the medusae of A. victoria and P. gregarium frequently occurs in the plankton, and because aggressive encounters between benthic hydrozoans are highly discriminatory and regulated at both interspecific and intraspecific levels, I conducted experiments with A. victoria and P. gregarium to determine the outcome of predatory interactions between hydromedusae and heterospecific embryos and planula larvae, and also between hydromedusae and genetically related or unrelated conspecific embryos and planulae. My purposes were (1) to determine if predatory interactions between planktonic life history stages of hydrozoans might parallel the aggressive interactions observed between benthic hydrozoan colonies, and (2) to determine if predatory interactions might occur not only between medusae of these species, but also between medusae and embryos or planulae. The results are discussed both in terms of population regulation of A. victoria and P. gregarium, and as regards evolution of intraspecific aggression in different life-history stages of species with complex life cycles.

MATERIALS AND METHODS

PREDATORS AND PREY

Sexually mature (adult) Aequoria victoria and Phialidium gregarium medusae were hand-dipped from surface waters near Friday Harbor Laboratories (Washington), sexed by examination of gonads under a dissecting microscope, and each placed in a jar containing 500 ml of 3 um-filtered seawater. Adult A. victoria were ca. 6 cm in diameter, while adult P. gregarium were ca. 3 cm in diameter. The jars were placed in a 10° C incubator the day prior to experiments, and the photoregime set so that both species of medusae spawned the following morning (see Miller, 1980). Throughout treatment, medusae were handled gently with plastic or glass and were not lifted out of water; medusae handled in this way

survived unfed for 1-2 wks in the laboratory and appeared healthy during the first several days following collection, though their tentacles became very long after 3-7 days of starvation (see Mills, 1981b), and the swimming bells became progressively smaller thereafter. On the day of experiments (one day following medusa collection) eggs and sperm from individual medusae were mixed, producing embryos of known parentage. Usually (see below) embryos were dyed for 2 min by adding 2-3 drops of 0.01% Neutral Red vital stain to 50 ml seawater containing the embryos. The stain facilitated discrimination of prey added at the beginning of experiments from eggs spawned by females during experiments.

PREDATION BETWEEN MEDUSAE

An experiment was conducted to determine that adult A. victoria would eat adult P. gregarium in the experimental setup. Two P. gregarium were placed in each of 5, 1-l jars nearly full of 3 um-filtered seawater. One A. victoria was added to each of the jars, which were then capped and strapped around the horizontal axis of a "grazing wheel" (see Yen, 1982; Bailey and Batty, 1983). The grazing wheel rotated slowly (ca. 1.6 rpm), keeping the predators and prey suspended. Experiments were conducted for 24 h in a 12:12 h light:dark 11° C coldroom, after which the number of surviving animals were counted. No controls were included in this experiment because handling errors and background (non-predatory) mortality did not occur.

A number of qualitative experiments were also conducted in unstirred 3.8 l jars or larger buckets to observe predatory interactions between pairs of heterospecific medusae in individual jars, or between groups of medusae over periods of 1-2 wk.. Seawater in the jars or buckets was partly replaced with 3 um-filtered seawater every few days, but medusae were not otherwise fed.

INTERSPECIFIC MEDUSA/PLANULA PREDATION

Most experiments with embryos and larvae were similar to those described in Pennington and Chia (1984 [Chapter IV], 1985 [Chapter V]) and Rumrill et al. (1985), which examine other aspects of predation upon larvae of benthic invertebrates.

Two experiments were conducted with heterospecific predator-prey combinations. In the first experiment, A. victoria medusae were offered P. gregarium embryos and planulae as prey, while in the second experiment P. gregarium medusae were offered A. victoria embryos and planulae. For experiments either 50 (A. victoria as prey) or 25 (P. gregarium as prey) cleaving embryos were counted into each of a series of 15, 1-l jars nearly full of 3 um-filtered seawater. The jars were divided into 3 sets (sets #1-3) of 5 replicates each. Sets #1-2 received dyed embryos, while set #3 received normal transparent embryos. In the first experiment one adult A. victoria was added to each jar of sets #2-3 (containing P. gregarium embryos). In the second experiment the converse procedure was performed, offering adult P. gregarium embryos and planulae of A. victoria as prey. In both experiments the jars in set #1 received no predators and controlled for background prey mortality and handling errors. Both dyed and normal embryos were offered to predators to control for possible artifacts associated with the stain; in subsequent experiments only dyed embryos were used.

Experiments were conducted on the grazing wheel as described above for predation between medusae. At the end of experiments medusae were removed and prey were concentrated by siphoning most of the water off through 73 um Nitex mesh. Surviving embryos had developed into planula larvae by this time; these were fixed and counted later. A one-way analysis of variance (ANOVA) was calculated with log-transformed data for each predator species, testing for significant differences between control values and values for treatments with predators; a t-test tested for differences in rate of predation on dyed or transparent embryos and planulae.

INTRASPECIFIC MEDUSA/PLANULA PREDATION

Three experiments were conducted to examine predation by medusae upon conspecific embryos and planulae. In the first experiment male and female A. victoria adults were offered their offspring as prey. Fifty dyed embryos from two parents were counted into each of 3 jars. This procedure was repeated 5 times with offspring from different parent-pairs, so that the 15 jars consisted of 5 sets of 3 jars, each set containing sibling embryos. The father and mother were added to separate jars within each set of 3 just prior to the beginning of the experiment, while the third jar received no

predator and served as a control.

In the second experiment adult A. victoria males and females were offered 50 conspecific embryos and planulae from other parents. These embryos and planulae were presumably unrelated to the medusae used as predators unless it is supposed that medusae collected from the plankton on any given day are budded from the same polyp colony.

In the final experiment, male and female P. gregarium medusae were similarly offered conspecific embryos and planulae from other parents as prey. As with A. victoria, these embryos and planulae were presumably unrelated to the medusae used as predators.

All intraspecific predator-prey experiments were conducted and analyzed as described above for interspecific predation.

RESULTS

INTERSPECIFIC PREDATION

Adult Aequoria victoria ate half of the Phialidium gregarium medusae offered as prey on the grazing wheel (Fig. 1A). Variance in predation rate was very high in this experiment because some A. victoria ate both P. gregarium offered while others did not feed. For this reason a number of qualitative experiments were conducted to observe predatory interactions between individuals and groups of medusae over several days. It was found that some A. victoria did not eat P. gregarium even to the point of starvation. Additionally, after several days of starvation a few A. victoria were observed to capture and ingest conspecific medusae, but never to digest them. The ingested medusae were always regurgitated and released after several hours. These individuals were apparently unharmed, though their tentacles were often tangled.

Aequorea victoria medusae did not eat significant numbers of Phialidium gregarium embryos and planulae (Fig. 1B; ANOVA; $0.75>P>0.50$), but medusae of P. gregarium consumed over half of the A. victoria embryos and planulae offered (Fig. 1C; ANOVA; $0.025>P>0.05$). In neither experiment were there significant differences in rate of predation upon dyed and transparent embryos and planulae (t-test; $P>0.9$).

INTRASPECIFIC PREDATION

Adult A. victoria did not eat significant numbers of conspecific embryos and planulae (Fig. 2A-B; ANOVA; $0.50>P>0.25$). This lack of predation was not a function of predator sex (father or mother) or genetic relatedness between predator and prey (offspring or unrelated prey). Similarly, adult P. gregarium did not consume unrelated conspecific embryos or planulae (Fig. 2C; ANOVA; $0.75>P>0.50$). Neither male or female medusae ate conspecific prey; it was therefore considered unnecessary to offer offspring as prey to adult P. gregarium.

DISCUSSION

In jars on the grazing wheel adult Aequorea victoria ate adult Phialidium gregarium, and adult P. gregarium ate embryonic and larval A. victoria. Both species thus were capable of feeding during experiments though it is not known if the observed rates of predation are representative of those in the plankton (and see Pennington and Chia, 1984 [Chapter IV], 1985 [Chapter V]; Pennington et al., in press [Chapter III]). Interspecific predation of adult A. victoria on P. gregarium has been previously documented in the laboratory (Arai, 1980; Arai and Jacobs, 1980) and is common in the field (pers. obs.). P. gregarium is not known to attack other hydromedusae (Arai and Jacobs, 1980; pers. obs.). However, the subsequent observation that some A. victoria apparently do not eat adult P. gregarium even when starved had not been previously noted. Further, attempted cannibalism among adult A. victoria had not been observed (these observations were also of starving individuals). Unfortunately, it remains unknown if particular A. victoria were prone to attack conspecific medusae while others were not. These differences in predatory behavior may reflect differences in the abilities of individual A. victoria to recognize or attack either P. gregarium adults or conspecific medusae, or conversely, may reflect differences between individual prey. Although nothing is known of the mechanisms by which medusae capture other medusae, recognition of potential prey items presumably occurs at the cellular level via the chemoreceptors controlling nematocyst discharge (see Marsical, 1974; Hildeman et al., 1979). It is tempting to speculate that because such control is genetically determined the observed differences in predatory behavior reflect genetic differences between conspecific medusae. Our observations of predation

between medusae should not have been influenced because nematocyst discharge is partly under nervous control and is influenced by predator hunger (reviewed by Picken and Skaer, 1966; Marsical, 1974). All medusae were starved equally and usually to death during these experiments.

The observation that some starved A. victoria ingested but failed to digest conspecific medusae remains perplexing; perhaps the mechanisms that prevent medusae from digesting themselves also protected conspecifics. However, LeBour (1922, 1923) apparently observed successful cannibalism between hydromedusae. In any case our observations underscore Dawkins' (1976) characterization of cannibalism as a risky strategy; one wonders if A. victoria's ability to prey on heterospecific medusae may not result in occasional cannibalistic attacks.

When medusae were offered heterospecific embryos and planulae as prey, adult P. gregarium ate A. victoria embryos and planulae, but adult A. victoria did not eat P. gregarium embryos and planulae. We had considered it likely that both medusa species would feed in these experiments because (1) P. gregarium is known to eat small and poorly motile prey (Larson, 1985; Pennington and Chia, 1985 [Chapter V]; Pennington et al., in press [Chapter III]), while (2) A. victoria is known to eat adult P. gregarium (Arai, 1980; Arai and Jacobs, 1980; above). However, we have also found that A. victoria preys at low rates or not at all on weakly-swimming or immotile polychaete eggs, unhatched echinoid embryos and swimming echinoid blastulae and gastrulae (Pennington and Chia, 1984 [Chapter IV]; Pennington et al., in press [Chapter III]). If A. victoria nematocysts are not discharged in response to immotile or slowly-swimming prey, it would appear that the motility of P. gregarium embryos and planulae might be insufficient to cause discharge of A. victoria nematocysts. It is of some interest that while adult A. victoria prey on adult P. gregarium, adult P. gregarium prey on embryonic and larval A. victoria. Analogous "networks" of aggressive interaction have been postulated to maintain species diversity in tropical epifaunal communities (Buss and Jackson, 1979). Because we do not know the frequency at which the medusae of each species preys on the other species in the plankton, we cannot evaluate the importance of interspecific predation in population regulation. Nonetheless, such interactions might promote the apparently stable coexistence of these hydrozoan species.

Neither adult A. victoria or adult P. gregarium preyed upon conspecific embryos or planulae in experiments. In A. victoria this result is probably due to the relative immotility of its embryos and planulae, but in P. gregarium the surface chemistry of conspecific embryos and planulae apparently averts nematocyst discharge. Because adult P. gregarium did not eat genetically unrelated conspecific prey, it is unlikely that they might eat their offspring. The almost complete lack of aggressive interaction observed between the same or different life-history stages of conspecific individuals in the plankton stands in striking contrast to the aggression found among benthic cnidarians (reviewed by Buss et al., 1984). However, A. victoria and P. gregarium were chosen for use here because of their co-occurrence in the plankton; their polypoid stages are not well known (see Arai and Brinckmann-Voss, 1980) and aggression among polypoid colonies of these species has been investigated. Although intraspecific aggression has been found in all hydrozoan colonies examined to date (Buss et al., 1984), it is possible that polypoid A. victoria and P. gregarium do not exhibit either intraspecific or intraspecific aggression. It might also be argued that the competitive aggression of benthic colonies bears little relation to the predatory aggression of medusae. While this argument may be valid in an evolutionary sense (see below), both phenomena are mediated by the same or closely related sensor-effector systems (nematocysts and their sensors). Buss et al. (1984) emphasize that aggressive interactions in Hydractinia echinata occur via "site-specific cellular differentiation" of stolonal cnidoms; they have not apparently examined interactions between allogeneic polyps, and it is not clear whether polyp tissues, which always maintain a cnidom, are capable of historecognition or aggressive responses as observed in anthozoans. For anthozoans at least, Bigger (1980) has pointed out that the distinction between competition and predation is largely arbitrary.

There is some indication that the lack of intraspecific aggression among planktonic stages described here may also occur among other medusae. Buehrer and Tardent (1980) found that manubrial transplants were uniformly successful between two strains of Podocoryne carnea medusae that were incompatible as polyps, indicating that histoincompatibility reactions were not expressed between medusae. Bigger (1976, 1980) has also observed that Cassiopea xamachana schphistomae elicited a stronger aggressive response from an anthozoan than did medusoid C. xamachana. In this context our

observations of aggression between starving adult A. victoria are exceptional.

If benthic hydrozoans can discriminate allogeneic conspecifics from clone-mates, their pelagic stages might be expected to do so as well. That hydromedusae, with the exception of starving A. victoria, do not appear to exhibit intraspecific aggression is apparently an adaptive response. Several general explanations may account for this observation. First, planktonic habitats may be "undersaturated" (cf. Istock, 1967) so that hydromedusae are not resource (food) limited and intraspecific aggression is valueless. This circumstance probably did occur during the radiation of the Hydrozoa into the plankton (Istock, 1967), and may still occur during a portion of each spring (Edwards, 1973; Mackie, 1974). However, over most of the year hydromedusae are probably food limited (exploitation competition) as indicated by their ability to crop down prey populations (Huntley and Hobson, 1978) and their annual population declines (see Mills, 1981a). A second, more probable explanation may be that while planktonic environments have been characterized as relatively uniform (Cushing, 1976), they are spatially unstable. The benefits of both interspecific and intraspecific aggression in interference competition are restricted to circumstances where interaction between competitors occurs predictably and repeatedly so that energetic investments in competition are likely to produce future benefits. Even though hydromedusae are confined to one broadly defined (and resource-limited) habitat, as is the encrusting epifauna (Buss, 1979; Buss and Jackson, 1981), such strategies are untenable for zooplankton. As noted above, predation is presumably rare between conspecific medusae because of the difficulties inherent in cannibalistic strategies (Dawkins, 1976). The above argument probably accounts for the lack of non-predatory aggression between medusae, but adults should still benefit by eating allogeneic embryos and planulae. However, it may be that because allogeneic adults must spawn in close proximity (cm) if eggs are to be fertilized (Roosen-Runge, 1962) male parents in particular may stand significant chances of eating their offspring if egg cannibalism occurs. Alternately, at least in the case of P. gregarium, selection against aggression between conspecific medusae may not permit the sensors controlling nematocyst discharge to discriminate between the surface chemistry of conspecific embryos, planulae and adults, resulting in a lack of predation on all life history stages.

Figure VI-1. Mean numbers of prey (± 1 standard deviation) surviving experiments with heterospecific predators: (A) medusoid (adult) A. victoria offered 2 adult P. gregarium as prey; (B) adult A. victoria offered 25 P. gregarium embryos and planulae as prey; (C) adult P. gregarium offered 50 A. victoria embryos and planulae as prey. Legend to the abscissa is C = Controls (no predators present), S = Stained Prey, T = Transparent (unstained) Prey. See text for statistical analysis.

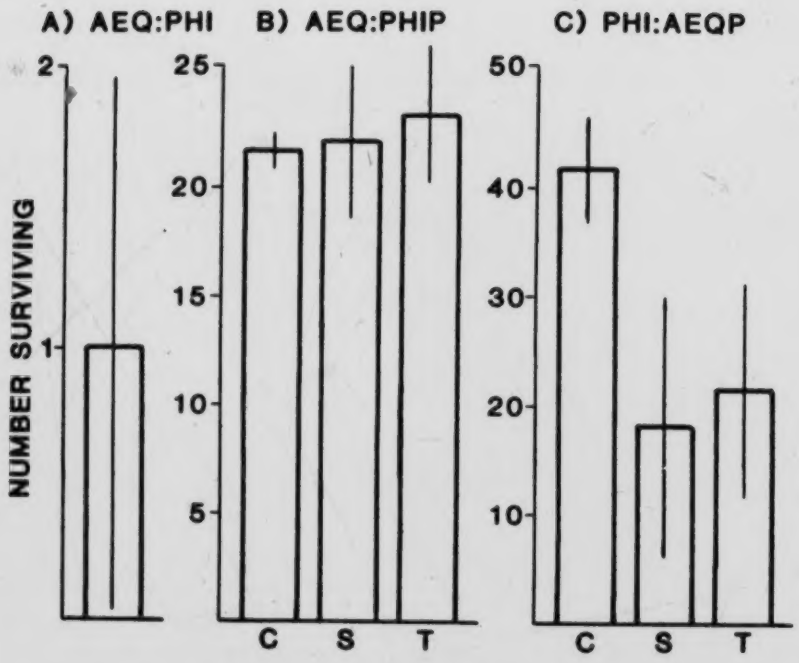
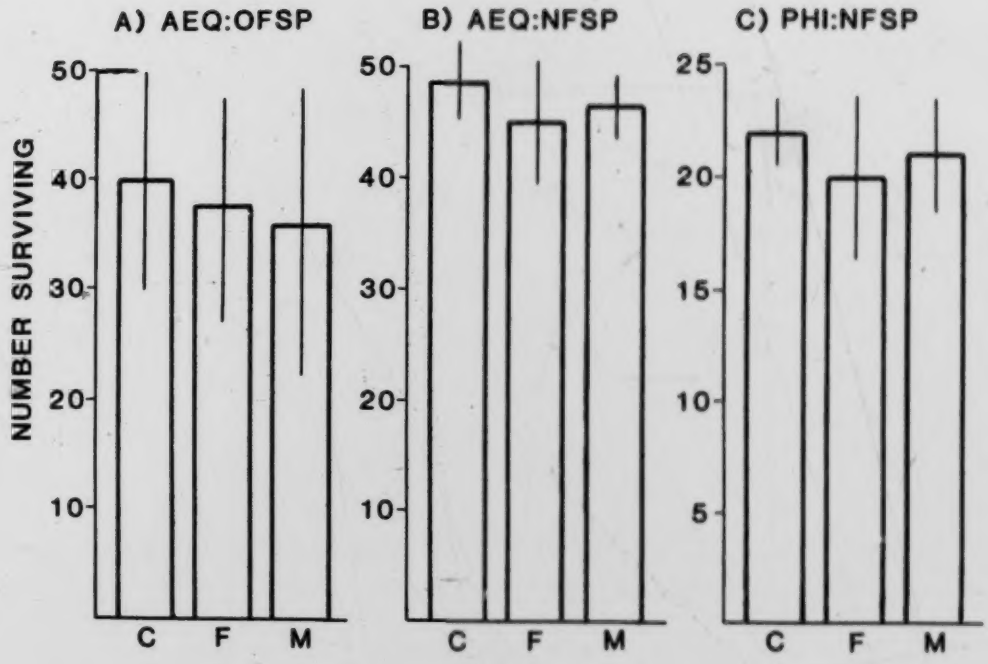

A) AEQ:PHI
B) AEQ:PHIP
C) PHI:AEQP
NUMBER SURVIVING
2
1
25
20
15
10
5
50
40
30
20
10
C
S
T
C
S
T

Figure VI-2. Mean numbers of prey (± 1 standard deviation) surviving experiments with conspecific predators: (A) medusoid (adult) A. victoria offered 50 of its offspring (embryos and planulae) as prey; (B) adult A. victoria offered 50 genetically unrelated embryos and planulae as prey; (C) adult P. gregarium offered 25 genetically unrelated embryos and planulae as prey. Legend to the abscissa is C = Controls (no predators present), F = Female Predators, M = Male Predators. See text for statistical analysis.


A) AEQ:OFSP
B) AEQ:NFSP
C) PHI:NFSP
NUMBER SURVIVING
50
40
30
20
10
25
15
5
C
F
M

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VII. CONCLUSIONS

This thesis has been devoted to examination of the pelagic life histories of larvae of benthic invertebrates. As noted in Chapter I, consideration of this segment of invertebrate life cycles has been dominated by Thorson's (1946) descriptive work and generalizations, and has largely been neglected by experimental scientists. In this thesis I have used descriptive methodology (Chapter II) to examine general population cycles of larvae, and experiments (Chapters III-VI) to examine particular problems concerning predation on invertebrate larvae (but also see Appendices A and B, following). In this concluding chapter I briefly review the results of the chapters as they pertain to one another, evaluate weaknesses of the work, and indicate some directions for future research.

Chapter II presents the results of a meroplankton survey. Although the value of this study lies primarily in its descriptions of seasonal occurrence and larval population dynamics in one locality, the broader trends were similar to those observed by a number of workers in European and other waters.

In the meroplankton survey the observed losses of 3-12% per day from larval stocks cannot, however, be attributed solely to predation - the subject of the remaining chapters. A number of factors in combination produced the observed losses, with local hydrographic features probably being the most important. Larval mortality due to predation is responsible for an unknown fraction of these losses. In part for this reason, the remaining chapters were not designed to estimate absolute rates of predation on larvae in the plankton. Instead, an artificial methodology which almost certainly affected overall rates of predation was used. The control provided by this methodology, however, permitted comparison of rates of predation on larvae between experiments, and I used this design characteristic to examine relative rates of predation on a number of larval types. Together with the data of Cowden et al. (1983), Rumrill and Chia (1985) and Rumrill et al. (1985), these chapters provide the first experimental documentation of patterns of predation on larvae of benthic invertebrates.

Thus experiments in Chapter III show that invertebrate predators ate few or no pluteus larvae of the echinoid Dendraster excentricus, but ate embryos and early larvae in large numbers. Two fish species, however, preyed heavily on later larvae. Because

predator / prey encounter rates are not known in the field (they were enforced in the laboratory), it was not possible to conclude what overall rates of predation on the respective larval stages might be in the plankton, even though this question is central to a number of mathematical models of larval life-history (e.g., Vance, 1973; see Strathmann, 1985). S.S. Rumrill is attempting to resolve this problem with a multidisciplinary approach, but for the present Chapter III provides unique demonstration that rates of predation by particular predator species are not constant through embryonic and larval development and suggests that particular patterns of predation on larvae may be expected from particular predator taxa.

A central question arising from Chapter III (and see also Greene, 1985) is whether or not the very diversity of marine planktivores might preclude the evolution of effective defenses among planktonic prey. Chapters IV and V address this problem by examining the utility of two putative larval defenses against a variety of predator types. In one case, larval setae of trochophores were found to deter all predators tested, but in the second case the torsion of larval gastropods resulted in little or no reduction in rates of predation. It thus appears that at least some defenses can be effective against the diversity of planktivores in the marine plankton; it is probable that gastropod torsion is not a defensive adaptation for larvae at all. Chapter IV additionally provides corroborative evidence for Chapter III in that, again, rates of predation were not constant through development and were generally lower on later larval stages.

Chapter VI documents patterns of predation among conspecific and heterospecific hydrozoan medusae, embryos and larvae. This chapter is in essence another examination of the specificity with which predator / prey interactions can evolve in the plankton. The observed lack of conspecific predation between potential competitors stands in contrast to the aggressive interactions observed between benthic hydrozoans; it is suggested this difference reflects the spatial instability of planktonic habitats. Heterospecific predation of medusae on embryos and larvae did occur, but in a direction opposite to that between adults of the two species examined, suggesting a mechanism that may promote coexistence between these species. While the results indicate that aggression between conspecifics is limited by the spatial instability of the plankton, they also demonstrate a high degree of prey selectivity by hydromedusae and reinforce the notion that the

plankton can be a biotically structured environment.

In summary, the meroplankton survey has provided the first broad overview of larval population dynamics in the northeast Pacific, and the experimental work has produced intriguing results concerning predator / prey interactions in the plankton. The experimental work has not determined, however, what portions of the larval losses observed in the plankton are due to predation. This discontinuity arises both from a lack of resolution in field data and from limitations associated with scale in the laboratory work. Because the laboratory experiments were conducted in jars of intermediate size, they have been treated as "black boxes" and the behavioral interactions of the predators and prey have not been observed (but see Rumrill et al., 1985). Conversely, it would also be of interest to conduct similar experiments in very large containers, either aquaria or enclosures (see Appendix B), which should more closely approximate conditions in the plankton.

The thesis represents my efforts to date to examine the ecology and evolution of pelagic invertebrate larvae. At the very least, the descriptive chapter should provide a broad outline of larval life histories, while the experimental chapters should demonstrate that experiments with pelagic eggs, embryos and larvae can be conducted to examine particular aspects of these life histories. It is my hope that the work will encourage others who are curious about the fates of invertebrate larvae in the plankton.

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VIII. APPENDIX A. THE ECOLOGY OF FERTILIZATION OF ECHINOID EGGS: THE CONSEQUENCES OF SPERM DILUTION, ADULT AGGREGATION AND SYNCHRONOUS SPAWNING

INTRODUCTION

[4] Success at fertilization is a critical step in the life-history of species, particularly for free-spawning marine invertebrates (Mortensen, 1938; Thorsen, 1946; Chia, 1974). Mortensen (1938) noted that although many asteroids produce enormous numbers of eggs, their rates of juvenile recruitment are typically low. He suggested that this discrepancy exists because the probability of eggs encountering sperm in the plankton is low, and that most eggs are never fertilized. In contrast, Thorson (1946) suggested that most eggs of benthic invertebrates are fertilized because adults of both sexes spawn nearly synchronously in aggregations, therefore insuring that sperm and egg encounters occur. In Thorson's (1946) view, low recruitment rates are largely due to predation upon embryos and larvae. Though Thorson's (1946) suggestion has since become most widely accepted, both ideas remain tenable because benthic invertebrates have rarely been observed spawning in the field, and because to date no study has determined field rates of fertilization for any free-spawning invertebrate.

I have thus examined conditions under which spawnings may, or may not, produce fertilized eggs of the sea urchin, Strongylocentrotus droebachiensis (O.F. Muller). First, laboratory experiments were conducted to examine the effects of sperm dilution and gamete age on percent fertilization (see Lillie, 1915, 1919; Cohn, 1918; Gray, 1928). Field experiments were then conducted to determine if adult aggregation and epidemic spawning might serve as effective counters to dilution of gametes by tidal currents and the effects of gamete aging. The echinoid S. droebachiensis was used in this study because: (1) it is a free-spawner, shedding its gametes directly into the sea; (2) adults are motile and can alter their proximity to one another; and (3) the prominent fertilization envelope, which quickly rises from eggs following fertilization (see Tyler and Tyler, 1966), is a convenient indicator of fertilization.

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[4]This appendix has been published: Pennington, J.T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Biol. Bull. 169: 417-430.

MATERIALS AND METHODS

LABORATORY EXPERIMENTS

The first series of laboratory experiments determined over what range of sperm concentration high percentages of fertilization occur. Gametes were obtained by intracoelomic injections of .55 M KCl. Two ml of freshly spawned but settled eggs were pipetted into each of a series of 10 jars containing 3 l of filtered seawater, resulting in a concentration of about 3 X 10^4 eggs per liter. The water in each jar was thoroughly stirred with a paddle which oscillated at about 20 cycles per minute (Strathmann, 1971). Freshly spawned undiluted semen, or "dry sperm", was quickly run through a series of 10, 10-fold dilutions, thus diluting the dry sperm by an order of magnitude at each step. One ml of each dilution was then added to a single jar of the series; the egg / sperm mixtures were allowed to incubate for 10 minutes before eggs were siphoned off, concentrated and fixed in 2% formalin. Assays for percent fertilization were made by counting the number of elevated fertilization envelopes on the first 100 eggs encountered under 160X magnification. Four replicates of this experiment were conducted. Absolute sperm concentrations were assessed by hemocytometer counts of sperm in water from each of the jars.

A second series of laboratory experiments determined the effects of gamete age after spawning on percent fertilization. In experiments to examine sperm longevity, dry sperm was quickly run through 4, 10-fold dilutions. One ml of the most dilute suspension was then added to each of a series of 7 dishes containing 50 ml of filtered seawater at time 0. One ml of settled eggs was added to the first dish at time 0, and in sequence to the remaining dishes at 10 minute intervals thereafter. The eggs added to each dish thus encountered sperm of different ages. Eggs were also added to one jar without sperm to serve as a control against inadvertant contamination of eggs by sperm. The egg / sperm mixtures were allowed to incubate for 10 min before they were fixed, and assays for percent fertilization were performed as above. Three replicate experiments were conducted.

Experiments to examine egg longevity were the converse of those described above for sperm. One ml of settled eggs were added to the dishes at time 0, and fresh

sperm dilutions (as above) were added in sequence to each of the 8 dishes at 10 minute intervals. The freshly diluted sperm added to each dish thus encountered eggs of different ages. The egg/sperm mixtures were incubated for 10 minutes prior to being fixed and assayed for percent fertilization as above. Three replicate experiments were conducted.

A final laboratory experiment was conducted to determine if high percentages of fertilized eggs would result from induced spawning in an aquarium. A 55 gallon aquarium was filled with filtered seawater and allowed to warm to room temperature (14°C). Sea urchins were injected with KCl solution, and when a male and female began spawning they were strapped, mouth down, to plexiglass plates and rinsed. The plates were then placed 50 cm apart on the bottom of the aquarium. The water within the aquarium was not mixed. Samples of eggs were pipetted from the female's aboral surface at 5 minute intervals during the first 20 minutes after spawning began, and also 20 and 24 hours later. Assays for percent fertilization were performed as described above.

FIELD EXPERIMENTS

Field experiments examined the effects of adult aggregation, current, and epidemic spawning on percent fertilization. A subtidal valley bordering San Juan Channel, Washington, was located where the tidal current usually flows in the same direction and where Strongylocentrotus droebachiensis is common about 10 m deep. The bottom of the valley consisted primarily of fist-sized cobble. A five meter transect was set up along the bottom running directly downcurrent. Current direction was determined by releasing dye, and current speed was estimated by timing dye movement along the transect. Several S. droebachiensis were collected from the vicinity and stimulated to spawn with KCl injections in situ. In initial trials, when a female began spawning she was moved upstream of other spawning animals and samples of eggs were pulled directly from over the gonopores into each of 12, 60 ml syringes. A spawning male was then placed at the head of the transect, and any other spawning sea urchins were moved well downstream. Along the transect at a series of distances from the spawning male, 10 ml of water were pulled into each syringe about 10 cm over the substrate. The first syringe was filled upstream from the male as a control to detect any extraneous sperm, the second was filled directly over the male's gonopores to assess maximal fertilizability of the eggs, and one syringe

each was filled at 10, 20, 40, 60 and 80 cm, and 1, 2, 3, 4 and 5 m downstream from the spawning male. Except for the control, the syringes now presumably contained both eggs and sperm; the syringes were then taken to a skiff where their contents were fixed after incubating a total of 10 minutes. Eggs within the syringes were later assayed for percent fertilization as described for the laboratory experiments. In later trials, the number of eggs per syringe was controlled by adding .08 ml of settled eggs (about 1600 eggs) to each syringe in the laboratory about an hour prior to performing the field experiments.

Similar experiments were conducted under a variety of current conditions, ranging from slack tide with little current (0.05 m/s) to swift currents (0.8 m/s) to examine effect of current on percent fertilization. Experiments as above were also conducted which simulated limited epidemic spawnings, using 3 spawning males at the head of the transect.

QUESTIONAIRE

Because only one direct observation of echinoid spawning was found in the literature (Randall et al., 1964), over 100 sets of questionaires were mailed to individuals and marine stations in North America, asking for information regarding diver observations of echinoid spawnings. Intertidal observations of spawning were not solicited because osmotic or thermal stresses associated with exposure to air may induce abnormal spawnings (Fox, 1924; Harvey, 1956), and it is doubtful that gametes or embryos survive at low tide in the intertidal zone.

RESULTS

LABORATORY EXPERIMENTS

In laboratory experiments to examine the effects of sperm concentration on percent fertilization, high percentages of fertilization were achieved only with relatively dense sperm suspensions (Fig. 1). Over 80% of the eggs were usually fertilized in suspensions containing more than 10^6 sperm/l, but percent fertilization rapidly declined in more dilute sperm suspensions until essentially no eggs were fertilized in suspensions containing less than 10^4 sperm per liter. Percent fertilization thus rapidly declined when dry sperm was diluted by 6-8 orders of magnitude.

In experiments to examine gamete longevity, diluted sperm suspensions lost potency rapidly so that less than 10% percent fertilization resulted when eggs were added to 20 min old sperm (Fig. 2A). Eggs, on the other hand, remained fertilizable for at least 90 min after spawning (Fig. 2B).

Results of the experiment to examine fertilization in still water indicated that little fertilization occured during the first 20 minutes following spawning in extremely still water, but that under these conditions some fertilization continued to occur even 24 hours later (Fig. 3).

FIELD EXPERIMENTS

Results of the initial series of field experiments show that percent fertilization fell rapidly with increasing distance from spawning males (Fig. 4). Eggs were never fertilized in the control sample taken upstream of the spawning male, whereas over 90% were usually fertilized in the syringe from directly over the spawning male. At distances greater than 10 cm downstream from the male fewer than 25% of the eggs were fertilized, and at distances over 1 m, 10% or fewer of the eggs were fertilized. These low rates of fertilization clearly indicated that the numbers of sperm were limiting, and therefore that the number of eggs per syringe should be controlled; in subsequent experiments constant numbers of eggs were added to the syringes prior to conducting field experiments. Figure 6A shows that this precaution did not substantially alter the results (for a similar result see Lillie, 1915).

The effect of current on percent fertilization was examined by conducting experiments in fast or slow-moving water. In fast current (>0.2 m/s; Fig. 5A), percent fertilization was lower at all points downstream than in slower currents (<0.2 m/s; Fig. 5B). However, in both cases percent fertilization declined with increasing distance from the spawning male. At distances over 1 m, percent fertilization was generally less than 20%, even in the slowest currents encountered.

In the simulated epidemic spawnings, percent fertilization was higher at all distances downstream from three spawning males in comparison to experiments where one male was used (Fig. 6A-B). Percent fertilization again decreased with increasing distance from the spawning males, and fewer than 50% of the eggs were fertilized at

distances greater than 1 m downstream when three males were used.

QUESTIONAIRE

Only seven direct observations of sea urchin spawnings were received in response to the questionaire, probably reflecting the rarity with which echinoids are observed spawning in the field. These observations and the published account (Table I) include four observations of spawning in aggregations and four observations of scattered spawning by a few individuals. These few observations indicate that sea urchins do not always spawn while aggregated.

DISCUSSION

The results of the laboratory experiments indicate that both dilution of sperm and its limited longevity can reduce percentages of fertilization; similar observations have been reported previously (e.g., Lillie, 1915, 1919; Cohn, 1918; Gray, 1928). It appears that 30-40 sperm for each egg were required to produce high percentages of fertilization (Fig. 1). Several workers have noted similar requirements (Gemmill, 1900; Branham, 1972; Sprung and Bayne, 1984; etc.) which are probably due to the kinetics of random sperm and egg encounters (Rothschild and Swann, 1951). The short potent life of diluted echinoid sperm (Fig. 2) is known as the "respiratory dilution effect" (reviewed by Chia and Bickell, 1983). In essence, sperm in dense suspensions remain quiescent as in the testis, but with dilution the sperm become increasingly active and are rapidly exhausted. Both of these factors restrict the conditions under which field spawnings might produce high percentages of fertilization. Sperm must not only be dense, but must be spawned (or diluted) only minutes prior to encounters with eggs.

In the field, percent fertilization was generally low at distances over 10 cm from spawning males. In laboratory experiments dry sperm diluted by 6-8 orders of magnitude produced similar percentages of fertilization. However, even in the slowest currents encountered, sperm was less than 10 minutes old before it drifted beyond the end of the transect. The limited longevity of diluted sperm thus did not affect results of experiments, and the decreases in percent fertilization observed were probably due to dilution alone. Even if the sperm were long-lived, they would probably be so quickly diluted after

spawning that encounters with eggs in the plankton would be rare in any case. The results of all field experiments indicate that if males and females spawn at distances of even a few meters from each other, percentages of fertilization will be very much reduced in comparison to animals that spawn in close proximity.

In all field experiments the syringes contained enough eggs to, in effect, estimate sperm density in the surrounding water. I was thus unable to examine rates of fertilization under conditions where egg suspensions were very dilute. If females spawned some distance upstream from males, possibly inducing downstream males to spawn with a water-born pheromone (see Reese, 1966; Giese and Pearse, 1974), higher sperm to egg ratios per unit volume of water downstream from the males might allow higher percentages of fertilization to occur in these areas. However, because echinoid sperm only swim about 2 cm during their potent life (Gemmill, 1900) and do not detect eggs at a distance (reviewed by Rothschild, 1956; Chia and Bickell, 1983), only those eggs that drift directly past spawning males should be fertilized; eggs drifting elsewhere should not encounter sperm.

Percentages of fertilization in slow currents were higher than in swift ones (Fig. 5), presumably due to the increased rate of dilution of sperm in swift-moving water. However, if sea urchins spawn into extremely still water, laboratory results indicate that little fertilization would occur (Fig. 3). Eggs and sperm simply accumulated on the aboral surface of the spawning animals and did not mix, resulting in low rates of fertilization. Because the sperm remained undiluted on the aboral surface of the male, it remained potent and continued to fertilize at least some eggs for 24 hours after spawning began. These results are almost certainly laboratory artifacts; such extremely still water should rarely, if ever, occur in neritic habitats. In summary, the above results indicate that higher percentages of fertilization in the field will occur if free-spawning animals spawn into quiet, rather than swift-moving water.

When epidemic spawnings were simulated by placing three spawning males at the head of a transect, water downstream presumably contained more sperm per unit volume and thus percentages of fertilization were higher at all distances from the males (Fig. 6). As circumstances that produced high sperm densities also produced the highest percentages of fertilization, percent fertilization would probably be still greater if larger

numbers of spawning males had been used.

It therefore appears that adults must first aggregate and then spawn synchronously if high percentages of fertilization are to occur. Mortensen (1938) did not believe that most asteroids exhibit such social behaviors, although at least 3 asteroid species aggregate or even pair during spawning seasons (Mortensen, 1931; Clemente and Anicete, 1949; Kubo, 1951). In contrast, Thorson (1946) suggested that synchronous spawning of local adults occurs among most species of free-spawning invertebrates. Thorson (1946) based his predictions largely on observations of laboratory spawnings, where a variety of stresses can cause spawning (Fox, 1924; Harvey, 1957) and where aggregation is typically enforced.

Echinoids have often been reported in aggregations during spawning seasons (reviewed by Boolootian, 1966; Reese, 1966), but it has rarely been determined if sea urchins are actually attracted to conspecifics or if they have simply converged upon some common resource such as food, or shelter during daytime (Mortensen, 1943; Moore et al., 1963; Randall et al., 1964; Pearse and Arch, 1969). In the single study where conspecifics have been shown to actively aggregate (Dix, 1969), the behavior was not confined to the spawning season and it was suggested that Evechinus chloroticus aggregates not for spawning purposes, but for mutual protection. Tennent (1910) did report that Lytechinus variegatus found in groups were often spawned-out, while scattered individuals contained gonads in varying states of maturity. Direct observations of echinoids spawning in the field (Table I) indicate that sea urchins do not always spawn in aggregations. It therefore remains possible that echinoids do not aggregate preparatory to spawning. However, some echinoids do migrate into shallow water during spring and summer, becoming abundant in the shallow subtidal (Elmhirst, 1922; Orton, 1929; Stott, 1931). Echinoids have also been reported moving in feeding "herds" or "fronts" (Foreman, 1977; Mattison et al., 1977; Witman et al., 1982; etc). Whether or not these behaviors are truly social interactions, if sea urchins spawn during periods of high population density, higher percentages of fertilization should result than if they spawn while scattered.

Although all experiments simulated synchronous spawnings, the brief potent life of dilute sperm and the absence of fertilization in control syringes filled upstream of

spawning males both suggest that no fertilization would occur if spawning was asynchronous. However, the observations in Table I indicate that synchronous local spawning is typical. Presumably, local environmental cues synchronize gametogenic cycles and induce spawning ("proximal causes"; Baker, 1939). In the field proximal cues have been suggested to be temperature and salinity changes or thresholds, lunar or tidal cycles, changes in quantity or quality of illumination and increases in phytoplankton or food abundance (reviewed by Giese, 1959; Boolootian, 1966; Giese and Pearse, 1974; Himmelman, 1981; Chia and Bickell, 1983). However, the effects of most proximal cues on spawning remain questionable because portions of a local population commonly become spawned-out weeks before others (MacGinitie and MacGinitie, 1949), and conversely, because spawnings frequently occur when there has been little or no change in a cue (Giese and Pearse, 1974). Some of the above confusion may arise because it has often been difficult to distinguish between factors that entrain gametogenic cycles and those that initiate spawning. Results of laboratory experiments to examine proximal cues as spawning inducers are difficult to interpret because spawning is often induced by exposing animals to stimuli in quantities that are potentially stressful to adults, gametes or embryos (Harvey, 1956; see Farmanfarmian and Giese, 1963; Andronikov, 1975; Greenwood and Bennett, 1981).

For echinoderms it is also unclear whether proximal cues might function by inducing entire populations to spawn, or whether they stimulate or stress a few susceptible individuals within a population to spawn. It is widely suggested that once spawning by one or a few animals is initiated, either the gametes or a pheromone released with them induce neighboring conspecifics to spawn (MacGinitie and MacGinitie, 1949; Hyman, 1955; Rothschild, 1956; Reese, 1966; Giese and Pearse, 1974; Kennedy and Pearse, 1975; Iliffe and Pearse, 1982). Fox (1924) and Lewis (1958) induced sea urchins to spawn by adding sperm suspensions to seawater in the laboratory, and Gemmill (1914, 1920) described similar experiments with starfish. However, many attempts to repeat these experiments have not resulted in spawning (Gemmill, 1900; Palmer, 1937; pers. obs.). In the field, Keckes et al. (1966) induced Paracentrotus lividus to spawn by exposure to homogenates of conspecific testes or ovaries, and two of the observations of spawning in Table I were made in the vicinity of sea urchins that had been crushed. In one

instance the crushed individuals were conspecific to those that were spawning, but in the second case crushed Strongylocentrotus franciscanus may have induced individuals of S. purpuratus to spawn. Nevertheless, several of the observations of Table I indicate spawning by only some individuals within a locale.

Though all free-spawning invertebrates encounter the problem of gamete dilution, there is certainly variation in the mechanisms utilized to increase percentages of fertilization. As one example, sperm of some hydromedusae and species of benthic invertebrates chemotactically sense conspecific eggs and swim towards them (Miller, 1979, in press). In this case it may be advantageous for sperm to be long-lived or even to remain quiescent until they sense nearby eggs. The evolution of blocks to polyspermy (see Rothschild, 1956) in eggs of free-spawning species clearly indicates that, at least occasionally, eggs encounter sperm in abundance.

In summary, the experiments presented here indicate that if free-spawning adults fail to aggregate prior to spawning, as Mortensen (1938) proposed, percentages of fertilization will often be low. Conversely, if they spawn in aggregations percentages of fertilization will be high, as Thorson (1946) suggested. It remains uncertain whether or not echinoids are gregarious prior to spawning, but it appears that local spawning is usually synchronous. If free-spawning invertebrates do not aggregate and then spawn synchronously, life-tables based on gonad indices or egg production may badly overestimate fecundity.

Table I. Summary of direct observations of subtidal echinoid spawnings. Unpublished personal communications were obtained as responses to over 100 sets of questionaires mailed to individuals and marine stations in North America.

Species	Season	Density (Ind./m²)	Physical Conditions	Spawning Behavior	Observer
Diadema antillarum	year-round	1.2-13.4	some current	individuals aggregate year-round; several observations of some individuals within a tight group spawning; upcurrent individuals seemed to spawn first	Randall et al., 1964, Caribb. J. Sci., 4: 421-433.
Lytechinus pictus	Summer	100-500	substantial current; high water temperature	no active aggregation; random individuals spawning; observed several years	R.C. Fay, Pac. Bio-Mar. Labs., Venice, California
Unknown (Apra Harbor, Guam)	Spring	75-100	slight current	strongly clumped; mass spawning	G. Pittenger, U.S.C. Mar. Lab., Avalon, California
Heliocidaris erythrogramma	Spring	0.1-0.5	no swell or surge; a rare, oily calm	clumped; eggs later seen floating as "rafts"	S.A. Sheperd, Dept. Fisheries, Adelaide, S. Australia
Stronglylocentrotus franciscanus	winter; early spring	unknown	slight current	no active aggregation; scattered individuals spawning	G. Dennis, Comox Diving Services, Comox, British Columbia
Strongylocentrotus franciscanus	unknown	ca. 5	little current or surge	dozens of individuals spawning near other conspecifics crushed by an anchor	J.S. Pearse, UCSC, Santa Cruz, California

Strongylocentrotus purpuratus	Spring	50-60	sea calm; no surge	no active aggregation; scattered groups spawning; crushed S. franciscanus nearby	C.T. Mitchell, MBC Applied Env. Sci., Costa Mesa, California
Strongylocentrotus purpuratus	Winter; Spring	20-100	moderate surge; low salinity	no active aggregation; random individuals spawning in December and January; mass spawning in April; crushed conspecifics did not induce spawning among intact individuals	R.C. Fay, Pac. Bio-Mar. Labs., Venice, California

Figure A-1. Results of four replicate experiments to determine percent fertilization of eggs when constant volumes of a series of 10, 10-fold dilutions of dry sperm (semen) was added to egg suspensions in stirred jars.

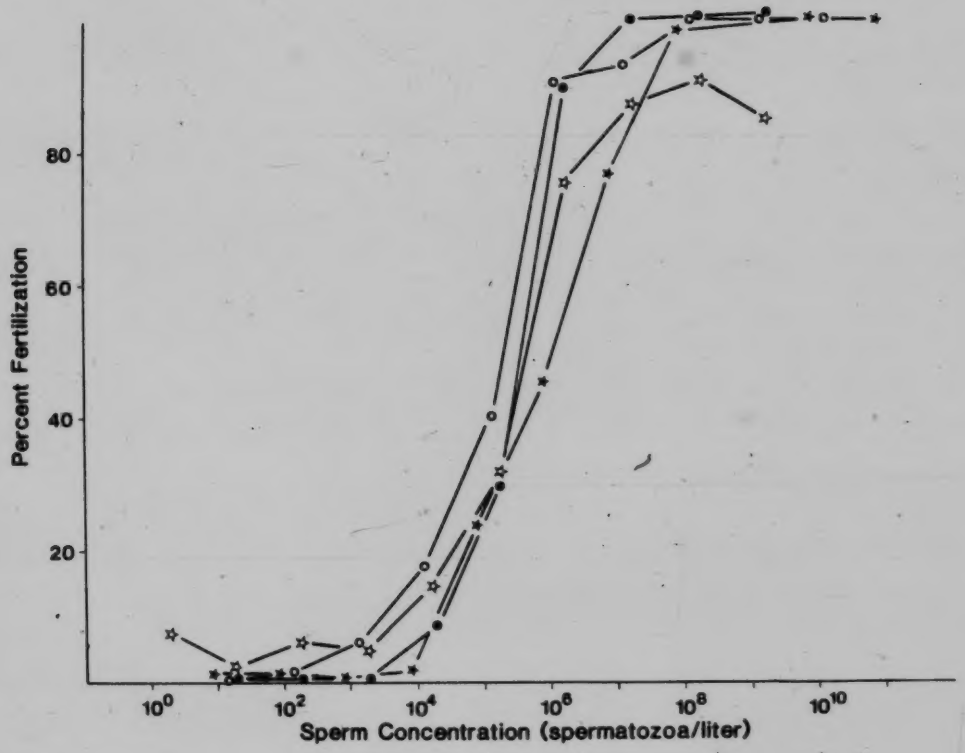

Percent Fertilization
80
60
40
20
10^0
10^2
10^4
10^6
10^8
10^{10}
Sperm Concentration (spermatozoa/liter)

Figure A-2. Mean percentages of fertilization (± 1 standard deviation) resulting from experiments to examine gamete longevity. In A, eggs were added to diluted sperm suspensions of various ages. B is the converse of A, where fresh sperm suspensions were added to eggs of various ages. Three replicates of each experiment were conducted.

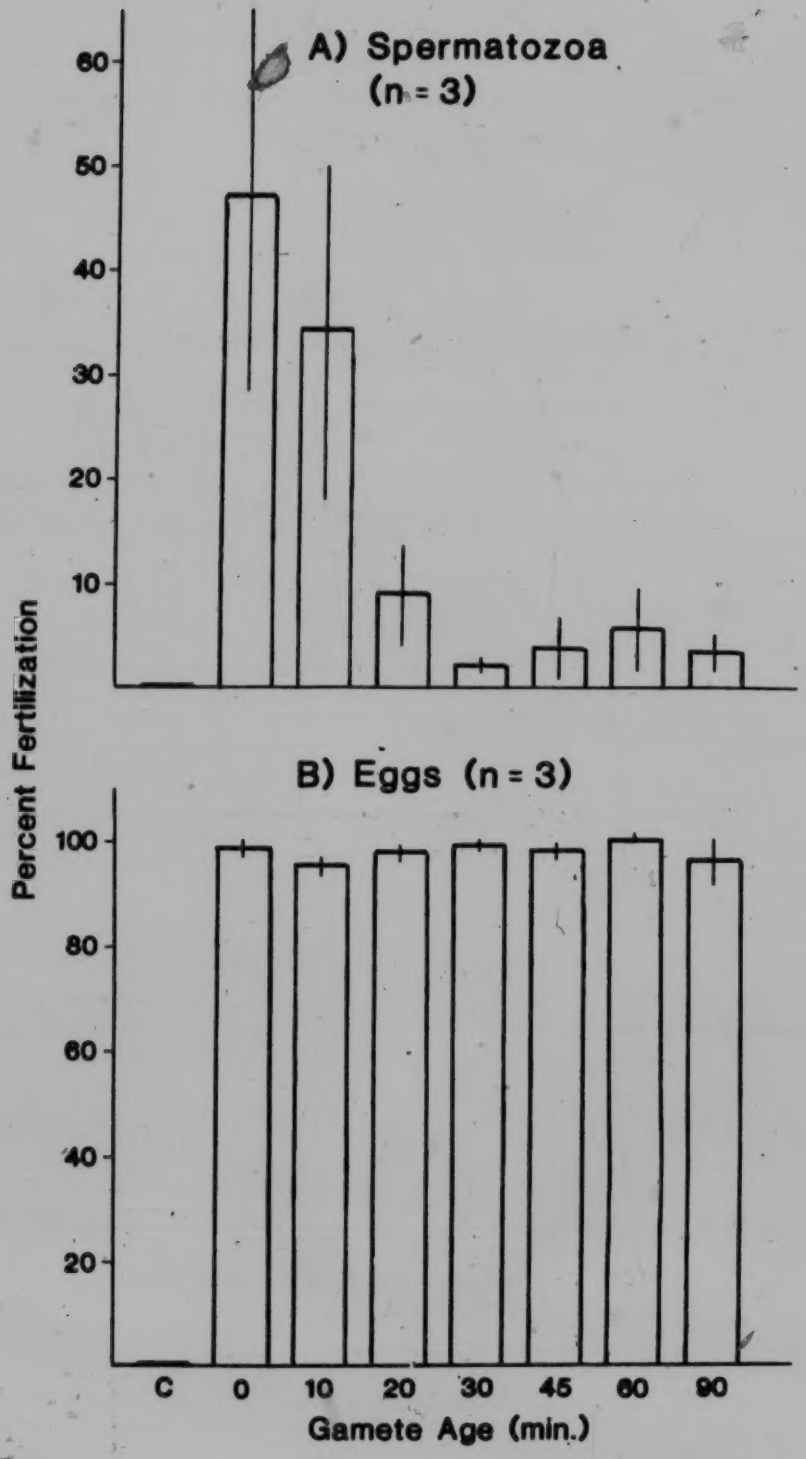

A) Spermatozoa
(n = 3)
60
50
40
30
20
10
B) Eggs (n = 3)
100
80
60
40
20
Percent Fertilization
C
0
10
20
30
45
60
90
Gamete Age (min.)

Figure A-3. Percentages of fertilization resulting from spawning of a pair of animals in still water. A male and female were induced to spawn, strapped mouth down to plexiglass plates, rinsed, and placed in an aquarium 50 cm apart. Eggs were periodically pipetted from the aboral surface of the female and assayed for percent fertilization.

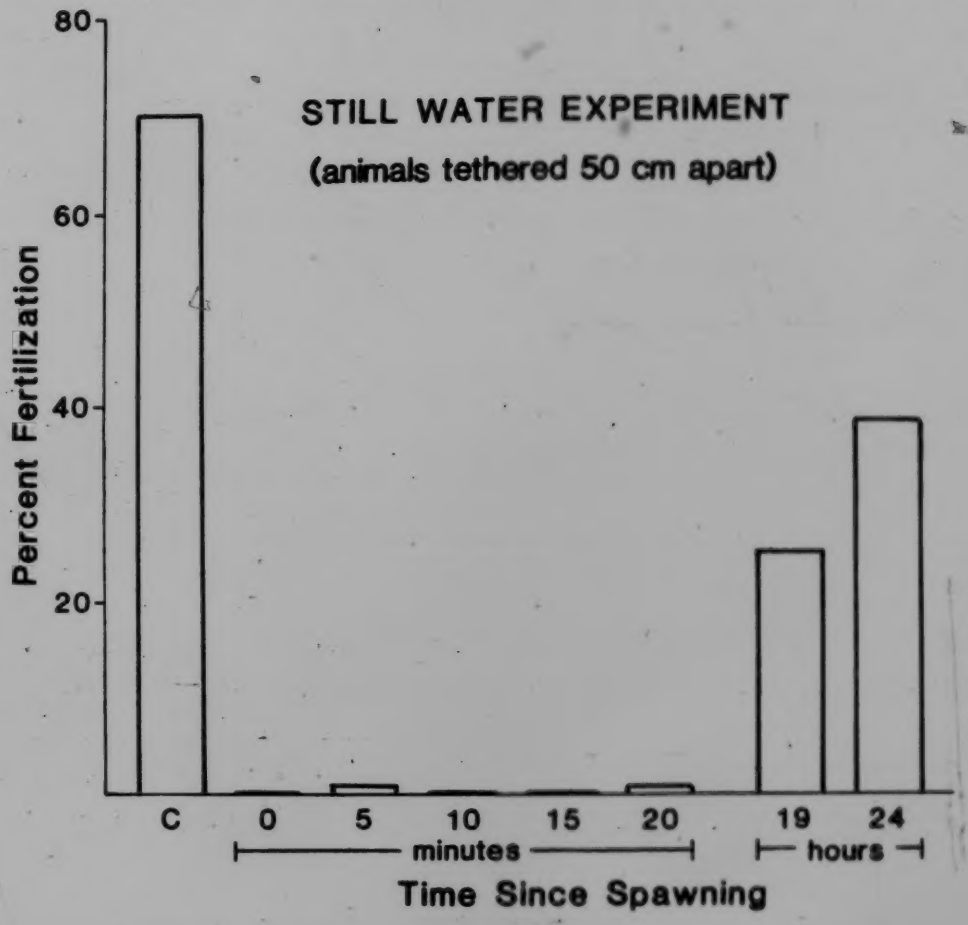

STILL WATER EXPERIMENT
(animals tethered 50 cm apart)
Percent Fertilization
80
60
40
20
C
0
5
10
15
20
19
24
minutes
hours
Time Since Spawning

Figure A-4. Mean percentages of fertilization (± 1 standard error) resulting from spawning by single males in the field. Eggs were drawn into the syringes in the field, and 10 ml of water was then pulled into the syringes along a transect running downcurrent from a spawning male. The number above each mean is the number of replicates conducted at that distance from the male.

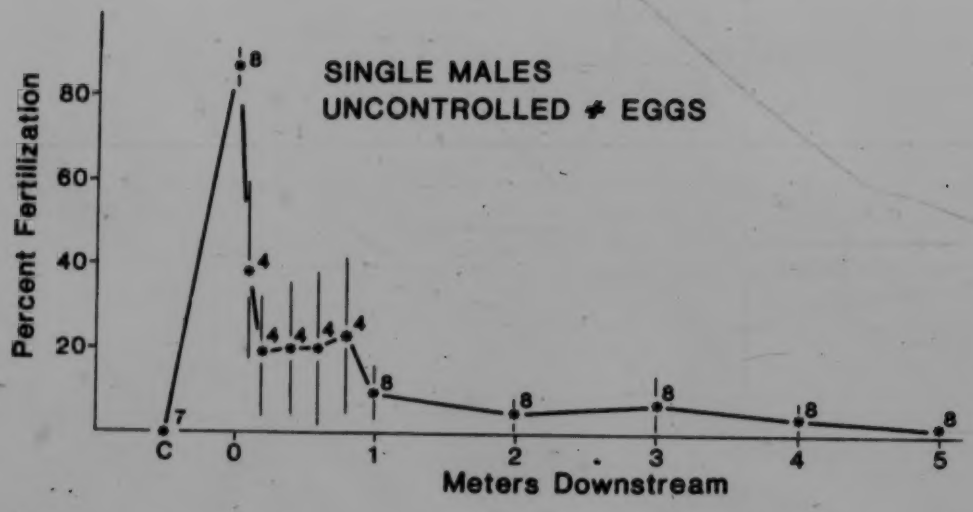

SINGLE MALES
UNCONTROLLED ♣ EGGS
Percent Fertilization
80
60
40
20
C
0
1
2
3
4
5
Meters Downstream

Figure A-5. Mean percentages of fertilization (± 1 standard error) resulting from spawning by single males in currents over 0.2 cm / s (A), or under 0.2 cm / s (B). Methods were the same as in Fig. 4. The number above each mean is the number of replicates conducted at that distance from the male.

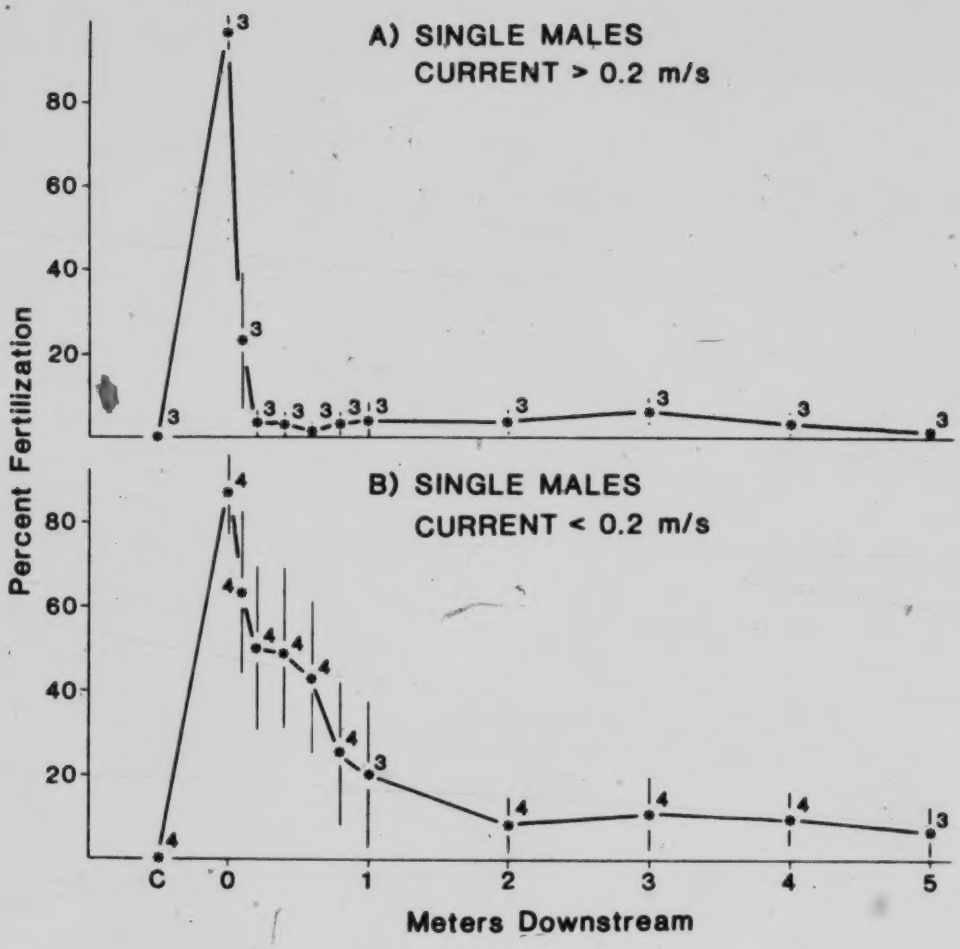
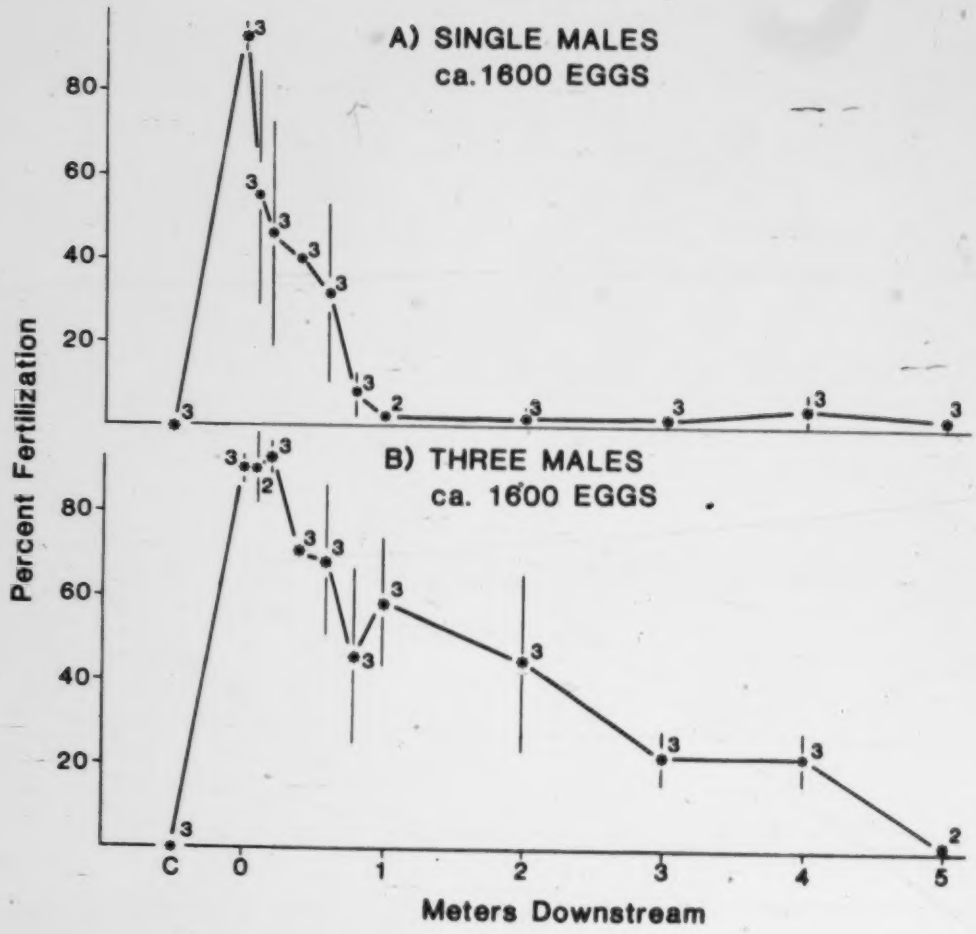

A) SINGLE MALES
CURRENT > 0.2 m/s
B) SINGLE MALES
CURRENT < 0.2 m/s
Percent Fertilization
80
60
40
20
C
0
1
2
3
4
5
Meters Downstream

Figure A-6. Mean percentages of fertilization (± 1 standard error) resulting from spawning by single males (A), or three males (B) at the head of the transect. Methods were the same as in Fig. 4, except that about 1600 eggs were pipetted into the syringes prior to experiments. The number above each mean is the number of replicates conducted at that distance from the male.


A) SINGLE MALES
ca.1600 EGGS
B) THREE MALES
ca. 1600 EGGS
Percent Fertilization
80
60
40
20
C
0
1
2
3
4
5
Meters Downstream

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IX. APPENDIX B. ONTOGENETIC AND DIEL VERTICAL MIGRATION OF A PLANKTONIC ECHINOID LARVA, DENDRASTER EXCENTRICUS: OCCURRENCE, CAUSES, AND PROBABLE CONSEQUENCES

INTRODUCTION

[3] Many types of zooplankton regulate depth and undergo both ontogenetic and diel vertical migrations (reviewed by Banse, 1964; Thorson, 1964; Meadows & Campbell, 1972; Crisp, 1974; Forward, 1976; Longhurst, 1976). For larvae of subtidal benthic invertebrates, ontogenetic migrations are suggested to be adaptive because they increase the probability of encounters with suitable benthic habitats. Diel vertical migrations of meroplankton have received less attention, but for zooplankton in general they are suggested to provide some control over rates of metabolism, feeding, encounters with predators, and dispersal.

To regulate vertical postition, a zooplankter must orient vertically, and move either up or down in response to environmental feature(s) indicative of depth (see Mileikovsky, 1973; Creutzberg, 1975; Sulkin, 1984). Orientation can be controlled by active sensory structures such as statocysts, or by passive mechanisms such as differential drag on body regions, spiral swimming or non-uniform body density (see Chia et al., 1984a). Vertical movements of invertebrate larvae have been shown in the laboratory to be controlled most often by light, but pressure, temperature and salinity are also used to to indicate depth. However, the effects of such environmental "cues" are not simple. For example, photoresponses are often altered by interactions between the above factors and larval age, nutritional state and sensory history (reviewed by Russell, 1927; Thorson, 1964; Forward, 1976; Sulkin, 1984). It is thus difficult to predict depth distributions of larvae in the plankton from laboratory experiments alone.

The depth-regulatory behavior of larvae of benthic invertebrates has received considerable attention. Thorson (1964) assembled some information on over 200 species of invertebrate larvae, and the topic continues to be of interest (reviewed by Forward, 1976; Sulkin, 1984; Young & Chia, in press). However, generalizations regarding

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[3] This appendix has been accepted for publication: Pennington, J.T. and R.B. Emlet. Ontogenetic and diel vertical migration of a planktonic echinoid larva, Dendraster excentricus (Eschscholtz): occurrence, causes, and probable consequences. J. Exp. Mar. Biol. Ecol.

depth-regulation are based largely on study of larvae of fouling animals (Thorson, 1964) and estuarine invertebrates (Strathmann, 1977); groups such as echinoderm larvae, which do not show obvious responses to environmental stimuli, continue to be neglected (Reese, 1966). Thorson (1964) discusses photoresponse in only two species of echinoid larvae, and these studies were misinterpreted. Theel (1892) did not state that Echinocyamus pusillus plutei are photopositive, but only that they swam to the surface. Similarly, Mortensen (1921) did not observe plutei of Laganum diplopora to be photonegative, but only to swim at the bottom of culture dishes. However, Neya (1965) described horizontal movmements of plutei of Hemicentrotus pulcherrimus in response to both horizontal and vertically-oriented beams of artificial white light. We are aware of no detailed examination of depth-regulation of any echinoderm larva.

We have studied depth-regulation in pluteus larvae of the sand dollar Dendraster excentricus (Eschscholtz). D. excentricus plutei are common in laboratory culture, but do not show obvious responses to environmental stimuli. We circumvented the interpretational difficulties encountered in laboratory studies of larval depth-regulation by first documenting the vertical distribution of D. excentricus plutei in the plankton, and also in a semi-natural enclosure and in a large outdoor aquarium. In combination these data permitted a simple series of laboratory experiments to determine which larval and environmental features cause the observed patterns of vertical distribution. Two final experiments examine a consequence of the observed diel vertical migration (DVM).

MATERIALS AND METHODS

FIELD OBSERVATIONS

Vertical distribution of plutei of Dendraster excentricus was examined in East Sound, Washington, on 6 days between May and August, 1983, as part of a study which documents the dispersal of plutei produced by a local adult population (Emlet, 1985). East Sound, a fjord-like embayment in the San Juan Archipelago, thermally stratifies during summer (King, 1976) and offers a restricted body of water with little tidal mixing. During daytime (0730-1530 hrs) a gasoline-driven diaphragm pump (5000 gal/h capacity) was used to collect 1 m^3 samples from depths of 1 m, 6 m and near the bottom between

10-15 m at several stations within East Sound. Samples were immediately filtered through 125 um mesh netting and preserved in 3% formalin. On August 22, temperature and salinity (American Optical temperature-compensated Refractometer) data were taken at a series of stations along the length of the Sound.

Samples were later split with a Folsom plankton splitter and half of each sample was sorted for D. excentricus plutei; these were identified by their fenestrated skeleton (Strathmann, 1979) and staged by their number of arms and development, if any, of the echinus rudiment (including juvenile test plates and spines; see Emlet, 1985). Plutei containing a well-developed echinus rudiment were termed "competent" to settle and metamorphose.

ENCLOSURE EXPERIMENT

A cylindrical enclosure constructed of flexible translucent plastic was suspended from the water's surface near a floating breakwater at Friday Harbor Laboratories, Washington, USA. The enclosure was 3.2 m deep, 1 m in diameter, and contained about 2500 l of filtered seawater.

For all experiments, embryos and larvae were cultured as in Highsmith (1982). For the enclosure experiment, eggs were fertilized at staggered intervals so that cultures of early and advanced 4-armed plutei, and 6 and 8-armed plutei were obtained simultaneously. High rates of development at summertime water temperatures (11-15° C) prevented the inclusion of hatched blastulae, gastrulae and prism larvae in this experiment. Additionally, it was not feasible to culture sufficient numbers of competent plutei to include them in the experiment. Larvae within a 20 ml subsample from each of 17, 3-l culture jars were counted to estimate the number of each of the above larval stages to be added to the enclosure. In total, approximately 620,000 plutei were added to the enclosure (ca. 250 larvae / l) at 0900 on the first day of the experiment, 3 h prior to the first sampling session. By stage, 50% of these were early 4-armed, 16% were late 4-armed, 31% were 6-armed and 6% were 8-armed plutei.

Sampling sessions were conducted at 1200, 1800 and 2400 hrs on the first day, and at 0600 and 1200 hrs of the second day of the experiment. During each sampling session, 3 replicate, 3-l samples of water and entrained larvae were collected with a

plunger-type pump from 0.1, 1.0, 2.0 and 3.0 m deep through a weighted garden hose hanging vertically 0.3 m from the inner wall of the enclosure. Water removed from the enclosure during sampling was not replaced. Each sample was immediately strained through 80 um Nitex mesh, and the retained larvae were washed into jars and fixed in 3% formalin. All larvae in each sample were later staged and counted, except that samples containing large numbers of plutei were subsampled with a Folsom plankton splitter so that at least 300 larvae were directly counted and staged. Light intensity (LICOR LI-185B Quantum Meter), temperature and salinity were measured at each depth during the sampling sessions.

AQUARIUM EXPERIMENT

An experiment similar to that in the enclosure was conducted in a large outdoor plexiglass aquarium. The aquarium was cylindrical, 1 m in diameter, 1.8 m deep, and its outside walls were wrapped with heavy black plastic. The aquarium was filled with about 1400 l of filtered seawater 24 h prior to the experiment to allow water and air temperatures to equilibrate (ca. 13° C). An estimated 240,000 4-armed plutei were added to the aquarium 19 hours prior to the first sampling session (ca. 170 larvae / l).

Sampling sessions were conducted at 1200 and 2400 hrs on the first day, and at 1200 hrs on the second day of the experiment. Sampling was conducted as in the enclosure experiment, except that samples were siphoned from 0.1, 0.5, 1.0 and 1.5 m deep. A black plastic cover was placed over the aquarium 12 h prior to the final sampling session. Samples were processed and larvae were counted as in the enclosure experiment. Light intensity, temperature and salinity measurements were taken at each depth during each sampling session.

LABORATORY EXPERIMENTS

Laboratory experiments were conducted to determine what larval or environmental features contribute to the observed patterns of vertical distribution, and in particular examined (1) how plutei orient vertically, (2) if ontogenetic depth distributions might be affected by changes in the specific gravity of embryos and larvae, and (3) if the diel migrations were caused by behavioral responses of embryos or larvae to thermal

discontinuities, visible light, or ultraviolet light. Additional experiments were then undertaken to determine whether growth and survival of plutei might be affected by exposure to ultraviolet light.

Vertical orientation

Distribution of body mass

The following experiment was conducted to establish that vertical orientation of plutei is due to asymmetrical distribution of body mass. The experiment was conducted with 4, 6, 8-armed and competent plutei, and also with hatched blastulae, gastrulae, and prism larvae. Embryos or larvae were killed by immersion in a 0.004% Nile Blue A:seawater solution for 15 min, after which the dye solution was washed away. This treatment killed larvae without apparent damage to larval tissues or form, and also stained the animals a vivid blue. Under a dissecting microscope, 50-100 individuals of each developmental stage were then floated in seawater over a sucrose solution (distilled water plus sucrose, see below) slightly denser than the embryos or larvae. The embryos and larvae were allowed to settle for 30 min into the density gradient produced by layering the two fluids, and the resulting vertical orientation of the embryos or larvae was noted. The vertical orientation of 5-10 individuals was then altered with a needle; if these returned to their original orientation it was concluded that asymmetrical distribution of body mass controls larval orientation.

Ontogenetic vertical migration

Larval specific gravity

The specific gravity of embryos, larvae and newly metamorphosed (20 h old) juveniles was determined by observing whether they floated on, or sank through sucrose solutions of different specific gravity. Animals were killed in Nile Blue and 50-100 individuals of each developmental stage (except competent plutei and juveniles, see below) were floated in seawater over a series of 10 distilled water:sucrose solutions ranging from 1:0.01 to 1:1.4 g H_2O:sucrose at about 20° C. After 30 min, if the animals had sunk through a particular sucrose solution to the bottom of the dish, it was concluded that they were denser than that solution. However, if they remained floating on the discontinuity

between the seawater and a sucrose solution, it was concluded that they were less dense than the solution in that dish. Experiments with competent plutei and juveniles were conducted as above, but with only 7 and 3 individuals, respectively. It was necessary to repeat experiments with these individuals several times, using different sucrose solutions. The specific gravities of the various solutions were obtained by reference to tables in the CRC Handbook of Biochemistry.

Diel vertical migration

Thermal discontinuities

The following experiment was conducted to examine the possibility that diel vertical migration (DVM) occurred because the plutei could not, or would not, swim up through a thermocline. A 25 cm tall plexiglass column, 1 x 3 cm in cross-section, was filled with seawater. Its lower half was immersed in a 12° C water bath while a hair dryer heated the upper half to 22° C. Thermometers fixed 10 cm apart in the upper and lower halves of the column monitored internal temperature. Little or no convection current disrupted the 10° C thermocline created in this way. Once the thermocline was established, about 100 4-armed plutei were gently injected through a port into the bottom of the column. If substantial numbers of plutei appeared at the top of the column within 30 min, it was concluded that the larvae swam through the thermocline. The experiment was conducted in ambient laboratory (fluorescent and indirect window) lighting.

Incandescent light

Experiments were conducted to examine the effects of incandescent light on both vertical and horizontal movements of plutei. To examine vertical movements, in a darkened room 50-100 4-armed plutei were pipetted into scintillation vials nearly full of seawater and allowed to swim to the surface. A tungsten-filament light source directed down into the vials from 10 cm above was then turned on (1050 uE / m^2 / s); this lamp produced white light containing both visible light (VIS) and UV-A (see below). After 20 min of illumination, any change in vertical distribution of the plutei was noted.

To examine horizontal movements, a small glass chamber constructed of microscope slides (2.5 x 2.5 x 7 cm) and nearly full of seawater was placed 30 cm from the light source (described above). In this case the light was directed horizontally through

the long axis of the chamber. Approximately 50 4-armed plutei were pipetted into the chamber, which was then stirred to distribute the plutei evenly along its axis. The horizontal distribution of the plutei was assessed following various periods of illumination. Possible effects of convection current created by heat from the light were assessed by observing dye movement in the chamber during illumination. Water temperature at both ends of the chamber was also measured to the nearest 0.1° C with a small thermocouple immediately after the light was turned off. These experiments were repeated over 10 times.

Ultraviolet light

To examine effects of solar ultraviolet light (UV) on the behavior of plutei, experiments were first conducted in sunlight, and then with artificial UV sources. Variously filtered UV lamps were used to examine (1) effects of intensity and spectrum, (2) effect on swimming speed and direction, and (3) developmental onset of response.

Pluteus behavior in response to sunlight was first examined by placing an uncovered glass jar containing 3 l of seawater and about 1000 8-armed plutei (with partially developed echinus rudiments) outdoors in direct but diffuse sunlight on a cloudy day. A control jar containing water and plutei was also set near a window in the laboratory (most transparent glasses and plastics filter UV <310-315 nm; see Jagger, 1965). Both treatments were thus exposed to similar amounts of light >315 nm, but only the outdoors plutei received shorter wavelengths. After 30 min, the vertical distribution of plutei within the jars was qualitatively noted. The jars that had been outdoors were then returned to the laboratory where the distribution of plutei was again noted after an additional 30 min. This experiment was repeated 3 times. Second, during a sunny afternoon (sun 30-45° off vertical; 690 uE / m^2 / s vertical irradiance 400-700 nm), 4 pairs of 100 ml polystyrene beakers filled with seawater and containing 100-200 plutei were set in direct sunlight. Two beakers were uncovered, while the remaining pairs were either covered with UV filters (Hoya HMC UV[0]), transparent plexiglass, or opaque plastic. After 20 min the vertical distribution of the plutei was noted. The beakers were then placed in a darkened 12° C incubator and the distribution of larvae again noted after 1 h.

Experiments were conducted with artificial UV sources after the methods of Damkaer et al. (1980) and Damkaer & Dey (1983). The UV spectrum has been arbitrarily

divided into UV-A (400-315 nm), UV-B (315-280 nm) and UV-C (<280 nm; see Damkaer et al., 1980). UV-C does not penetrate the earth's atmosphere. Because UV-B has greater effects on the photochemistry of biological systems than UV-A, the following experiments were conducted with lamps filtered to approximate the UV-B irradiance of sunlight at sea level (see Damkaer et al., 1980, 1981). The UV-A and visible light (VIS) emitted by these lamps was not controlled, but was less than that of direct sunlight (Damkaer & Dey, 1983). Some indirect light from the laboratory's windows and fluorescent fixtures was also present during experiments.

Double light fixtures containing one Westinghouse "cool white" fluorescent lamp and one FS-40 fluorescent "sunlamp" were mounted over 3 ml spectrophotometer cuvettes or scintillation vials filled with seawater and containing 10-100 4-armed plutei. For all experiments the light was filtered through cellulose triacetate plastic (CTA) to eliminate light below 290 nm. Relative UV-B intensity was measured with a Robertson-Berger Sun Meter. This instrument provides an estimate of "biologically effective" UV; its response to UV-B irradiance has been compared to other commonly used scales of biological effectiveness by Damkaer and Dey (1982). For experiments, intensity of UV-B radiation was adjusted by varying the thickness of the CTA filter and the distance between the light source and the water surface. UV-B intensity at the air-water interface of the cuvettes or vials was expressed as proportional to approximate solar UV-B irradiance at noon on a clear summer day at sealevel (half, full, or double; see Damkaer et al., 1980). All treatments were replicated at least 4 times, and at least 2 replicate vials or cuvettes covered with transparent (but UV-B opaque) plexiglass controlled for potential effects of UV-A and visible light on larval behavior.

In the first experiment with these lamps, 4-armed plutei were irradiated with either half, full, or double intensity UV-B (plus UV-A and VIS) for 25 min. Plutei were allowed to swim to the surface prior to irradiation. Their vertical distribution was qualitatively noted as the lamps were turned off and one hour later. A similar experiment with full intensity UV-B was quantified by counting 10 4-armed plutei into each of 6 cuvettes. The number of larvae within 1 mm of the surface, in the water column, or within 1 mm of the bottom was counted (1) before the lights were turned on, (2) after 20 min irradiation with full intensity UV-B, (3) after 5 min additional irradiation following a gentle tapping of the vials,

and (4) 1 h after the lights were turned off.

In another experiment, 4-armed plutei were irradiated as above, except that a 10 mil filter of Mylar plastic was used to remove wavelengths below 315 nm (as did the plexiglass over control cuvettes). The larvae were thus exposed to UV-A and visible light only. Four-armed plutei in quartz cuvettes were also irradiated with full intensity UV-B from below. Their vertical distribution was noted before and after treatment. Finally, hatched blastulae, gastrulae, prism larvae and 4, 6 and 8-armed plutei were each irradiated from above for 20 min with full intensity UV-B. In this case controls consisted of uncovered and plexiglass-covered cuvettes containing 4-armed plutei, as well as covered cuvettes containing the developmental stage under consideration. The vertical distribution of the embryos or larvae was noted both before and after irradiation.

Growth and survival of irradiated plutei

Brief exposure

To determine if the dosage of UV-B required to elicit the behavioral response might be harmful to plutei, fifty 4-armed plutei were counted into each of 6 shallow bowls (ca. 3 cm deep). Four bowls were then irradiated with full intensity UV-B for 20 min. Two bowls were not irradiated and served as controls. All 6 bowls were then placed in a running seawater bath (ca. 12° C) under ambient laboratory (fluorescent and indirect window) lighting, and survival and general appearance of the larvae was assessed 3 days later.

Chronic exposure

A final experiment assessed the effects of simulated solar UV regimes on plutei confined in shallow water. Fifty 4-armed plutei were counted into each of 50 shallow bowls (ca. 3 cm deep); these were divided into 5 treatments of 10 replicate bowls each. For 8 hours daily, each treatment was subjected to either: (1) half intensity UV-B (plus UV-A and VIS); full intensity UV-B (plus UV-A and VIS); (3) double intensity UV-B (plus UV-A and VIS); (4) UV-A and VIS; (5) ambient laboratory light only. The light sources were set up, and spectrum and intensity were controlled as described under "Ultraviolet light". The bowls were kept cool in a circulating water bath, and larvae were fed and their water changed on alternate days over the 8 days of the experiment. Every 2 days larvae in at

least 2 bowls from each treatment were fixed, counted, and examined for growth and general appearance.

RESULTS

FIELD OBSERVATIONS

The majority of both precompetent and competent plutei found during our field sampling occurred in surface waters (Fig. 1). These results are in general agreement with those obtained by Rumrill et al. (1985), who found echinoid plutei (unstaged) to be most abundant in shallow water. In the present work there was some variation in depth distribution among precompetent plutei with date and time of sampling (0730-1530 hrs); these differences are discussed elsewhere (Emlet, 1985). Nonetheless, over 1000 precompetent plutei were caught and 81% of these occurred 1 m deep. All 89 competent plutei that were found also occurred at this depth. These results indicate that plutei regulate depth, that they occur in shallow water, and that there was no ontogenetic vertical migration.

ENCLOSURE EXPERIMENT

During each sampling session, the vertical distributions of early 4-armed, advanced 4-armed, and 6 and 8-armed plutei in the enclosure were similar, but all stages underwent DVM over the 2 days of the experiment (Fig. 2). Variance in the number of larvae of a given stage caught between the 3 replicate samples taken at each depth during each sampling session was low (mean coefficient of variation, 23%), indicating that the samples provided repeatable estimates of the vertical distribution of larvae. However, number of larvae captured per liter during the first sampling session (170 larvae/l) was less than the estimated number initially added to the enclosure (ca. 250 larvae/l). The numbers of larvae captured subsequently declined so that only 61 larvae/l were taken during the final sampling session. These losses remain unexplained, but are apparently due to larval mortality, possible undetected leaks, and some minor loss resulting from our sampling without replacement. It is also conceivable that larval distributions were sufficiently stratified so that some sampling sessions underestimated number of larvae in the

enclosure; we have no evidence that such stratification occurred in this experiment. Nonetheless, enough larvae remained in the enclosure so that the minimum number of larvae of any stage captured during any sampling session was 78 (8-armed larvae, last sampling session); a mean of 710 larvae of each of the other 3 stages were sampled during this session.

Salinity was nearly uniform at all depths within the enclosure (28-29 ppt), but both temperature and light intensity increased in the enclosure during daytime, primarily in the upper 1 m (Fig. 2).

AQUARIUM EXPERIMENT

On the first day of the aquarium experiment (1200 and 2400 hrs), plutei underwent DVM as in the enclosure experiment (Fig. 3). During the 1200 hrs sampling session on the first day, the greatest larval density was at 1 m, rather than near the bottom as in the enclosure experiment. This difference may have occurred because the opaque walls of the aquarium shaded its lower portion, even at 1200 hrs. Twelve hours later, at 2400 hrs, the mean depth of the larvae was shallower and substantially more plutei were caught in the top meter of the aquarium than during daytime. However, as in the enclosure experiment, nearly equal numbers of larvae were also caught in deeper water. This result indicates that while larvae left the surface during daytime, their return at night was slow (mean rate of upward movement, 4.3×10^{-3} mm / s). During the 1200 hrs sampling session on the second day, after the top of the aquarium was covered with black plastic (first day, 2400 hrs), 78% of all larvae occurred at the surface.

Variance in number of larvae captured between the 3 replicate samples at each depth during each sampling session was again low (mean coefficient of variation, 12%). However, the mean numbers of larvae / l captured increased over the 24 hours of this experiment: means of 108 and 244 larvae / l were captured during the first and last sampling sessions, respectively. These figures bracket the estimated number of larvae initially added to the aquarium (ca. 170 larvae / l) and apparently reflect undersampling of larvae during the first sampling session, and oversampling of plutei which had accumulated near the surface during the last sampling session. The minimum number of larvae caught during any sampling session was 3892 (first sampling session).

As in the enclosure, both temperature and light intensity in the aquarium increased during daytime, primarily in the surface meter of water (Fig. 3). During the second day, however, the cover substantially reduced such increases. Salinity was nearly uniform throughout the aquarium (30 ppt). Some convection current was created by sunshine on the walls of the aquarium (ca. .3 mm / s); this current could not produce net vertical transport of larvae and did not appear to affect the DVM.

LABORATORY EXPERIMENTS

Vertical orientation

Distribution of body mass

When layered in seawater over a denser sucrose:distilled water solution, dead prism larvae and plutei uniformly settled onto the discontinuity between the two fluids with their arms upwards and posterior downwards (Fig. 4). Competent plutei also settled posterior down. When pushed over with a needle, all larval stages returned to this orientation within a minute. It thus appears that the center of larval mass is posterior and orients the larvae passively; with the anterior end uppermost any forward swimming results in geonegative movement. Most hatched blastulae and gastrulae also settled onto sucrose solutions with their antero-posterior axis vertical. It was not determined which end was uppermost.

Ontogenetic vertical migration

Larval specific gravity

Results of experiments to determine the overall body density of embryos, larvae and newly metamorphosed juveniles indicate that pre-pluteus stages are slightly denser than seawater, but plutei and juveniles are substantially denser (Fig. 5), presumably due to the development of the calcareous larval skeleton. However, 8-armed plutei, competent plutei and juveniles were substantially less dense than 4 and 6-armed plutei. It was noted that the digestive tissue of advanced-stage plutei became markedly yellow in color (see also Highsmith, 1982); the yellow material remained conspicuous in newly metamorphosed juveniles.

Diel vertical migration

Thermocline

During both the enclosure and the aquarium experiment, temperatures rose from 13° to 16° C near the water's surface during daytime (Figs. 2-3). This warm layer formed at the surface and was underlain by a thermocline that moved deeper during day, as did the larval distribution. It was therefore possible that the vertical migration occurred because the plutei could not, or would not, swim through a thermocline of about 3° into 16° C water. However, when about 100 plutei were introduced into the bottom of a 25 cm column with a 10° C thermocline (12-22° over 10 cm), almost all larvae quickly swam up through the thermocline and accumulated at the surface within 15 min, even though 22° C is approximately the maximum temperature at which these larvae can be successfully cultured. These results indicate that temperature effects did not cause the observed DVM.

Incandescent light

In experiments with intense incandescent light shining down into vials containing plutei, no movement of plutei away from the water's surface was observed. However, in experiments with the same light source shining horizontally through the long axis of a small chamber, plutei appeared to aggregate away from the end of the chamber nearest the light source (Fig. 6a). Even though plutei always swam up, a short period of exposure to the light (1-5 min) resulted in aggregations of larvae near the center of the chamber. Exposure for longer periods (>5 min) resulted in aggregations near the end of the chamber furthest from the light source.

The apparent weak response of plutei, to horizontal beams of light only, caused us to consider that convection currents created by the light's heat produced the aggregations. Using dye to observe water movement, it was found a 0.1° C difference in temperature between the ends of the chamber was sufficient to produce convection currents. The convection currents formed as circulating cells, first rising along the wall of the chamber closest to the light, then flowing at the surface away from the light along the axis of the chamber, and finally turning down and back towards the light as a replacement current (Fig. 6b). Because the plutei swam up, they were carried along in both upwards and horizontal currents. However, where the current of the convection cell turned downwards, the larvae continued to swim up but now against the current, and became

concentrated along a "downwelling front" within the chamber (Fig. 6c). When the chamber was illuminated for longer periods of time, the convection cell grew longer until the replacement current turned downwards at the end of the chamber furthest from the light source, producing aggregations of larvae there. Thus, the observed horizontal movements of larvae were not photoresponses, but resulted from interactions between larval swimming and convection currents.

Ultraviolet light

When ultraviolet light (UV) was considered as a potential cause of the observed DVM, experiments were first conducted in sunlight using windowglass and plastics as UV filters (see Jagger, 1965). Uncovered jars containing plutei were placed either outdoors, or behind a window in sunlight in the laboratory. Before the experiment, ca. 95% of the larvae were in the top 1 cm of water in the jars. After 20 min ca. 95% of the plutei outdoors had descended into the lower half of the jars while almost all of the plutei in the indoor jars remained at the surface. Thirty min later, after being returned to the laboratory, ca. 90% of the larve from the outdoors jars had swum back to the surface. The above experiment was repeated outdoors in beakers either uncovered, covered with UV filters, or covered with opaque plastic. After 20 min in direct sunlight, ca. 50% of the larvae in the uncovered beakers were on the bottom and only 10% were at the surface. In both covered beakers, ca. 80% of the larvae were at the surface after 20 min and none were on the bottom. The beakers were then moved indoors. One h later ca. 95% of the larvae in all the beakers were at the surface. These results indicated that a component of sunlight (UV-B) removed by the glass laboratory windows and the above filters apparently caused plutei to descend.

When irradiated with full intensity artificial UV-B (plus UV-A and VIS; see Methods), 4-armed plutei sank to the bottom of vials or cuvettes (Fig. 7). Plutei in control cuvettes covered with transparent (but UV-B opaque) plexiglass remained at the surface during all of the following experiments. The response in uncovered cuvettes was so striking that most of the following results were assessed qualitatively. However when quantified (Fig. 8), 70% of the plutei descended to the bottom of cuvettes after 20 min irradiation. Some plutei were invariably trapped at the water surface (see Hinegardner, 1969), but if the cuvettes were gently rocked or tapped most of these quickly sank to the bottom. One

hour following irradiation, most plutei had returned to the surface or were swimming in the water column. Plutei in control cuvettes covered with plexiglass remained at the surface during all experiments. Larvae similarly exposed to either double or half intensity UV-B also descended to the bottom of cuvettes. These experiments indicate that UV-B at natural intensities causes plutei to descend. However, when exposed to only UV-A and VIS, 4-armed plutei did not leave the water's surface. UV-A and VIS appeared to have no effect on larval behavior, though their intensities in these experiments were lower than those in direct sunlight.

When placed in quartz cuvettes and irradiated with full intensity UV-B from below, 4-armed plutei sank to the bottom of cuvettes towards the light source. Because this treatment did not produce a negative phototaxis but instead inhibited swimming, the response to UV-B appears to be kinetic.

Finally, irradiation with full intensity UV-B from above caused all pluteus stages to sink (except competent plutei; these were not available during UV experiments). No difference in response was observed between stages. However, hatched blastulae and gastrulae never left the water's surface when irradiated with UV-B, and prism larvae exhibited little, if any response. It thus appears that UV-B irradiation of the epidermal cells of pre-pluteus stages does not arrest ciliary activity.

Growth and survival of irradiated plutei

Brief exposure

Four-armed plutei irradiated for 20 min with full intensity UV-B exhibited no ill effects 3 days later. Survival was good in both irradiated and control treatments (Table 1). At the termination of the experiment, both irradiated and control plutei swam at the water's surface, appeared healthy, and had grown since the beginning of the experiment. This result suggests that the dose of UV-B required to elicit the behavioral response is not harmful to plutei, at least over 3 days.

Chronic exposure

In experiments to examine the effects of long-term exposure to UV photoregimes, survival of control plutei exposed to UV-A plus VIS or to ambient laboratory light was very high over the 8 days of the experiment (Fig. 9). However, all

larvae subjected to full or double intensity UV-B were dead by the 4th day of the experiment, and most larvae exposed to half intensity died by the 8th day. Equally important, by day 4 it was clear that plutei recieving half intensity UV-B were not developing normally; these larvae swam weakly at the bottom of dishes, appeared blotchy, and had not grown since the beginning of the experiment (Fig. 10). The results of this experiment suggest that chronic exposure to simulated UV-B photoregimes in surface waters can kill or retard development of plutei. However, "full intensity" UV-B approximated solar UV-B irradiance at noon; while plutei in this treatment were irradiated at realistic midday rates, the total dosage of UV-B in this treatment was high (8 h/da; see Damkaer & Dey, 1981). The "half intensity" treatment better approximated total daily dose of UV-B in surface waters. Additionally, under all the photoregimes UV-A and VIS were much less intense than in sunlight (Damkaer & Dey, 1983), potentially reducing rates of larval photorepair. These technical difficulties might be avoided by conducting similar experiments outdoors in direct sunlight.

DISCUSSION

VERTICAL ORIENTATION

Lyon (1906), Runnstrom (1918), Mortensen (1921) and Fox (1925) noted that echinoid embryos and larvae swim up to the water's surface in culture. Lyon (1906) found that the behavior in Arbacia punctulata plutei is a direct response to gravity and is not altered by visible light, temperature changes, or oxygen gradients, and Runnstrom (1918) stated that the thickened posterior skeletal rods of plutei "stabilized" their vertical orientation with posterior downwards. In Dendraster excentricus plutei, the posteriorly-directed asymmetrical distribution of body mass provides a passive and nearly infallible method of geo-orientation. With posterior downwards, any forward swimming results in geonegative movement. A variety of zooplankters, including some invertebrate larvae, have been suggested to orient in this way (reviewed by Rudjakov, 1970; Chia et al., 1984a), although the mechanisms by which zooplankton without statocysts orient vertically have rarely been examined (Creutzberg, 1975). Plutei do swim backwards if they encounter objects or are disturbed and they can also turn and swim horizontally, at least

for short distances (Strathmann, 1971). Nonetheless, on a larger scale most pluteus movements probably function to regulate depth, as has been suggested for other larval and zooplankton swimming (Hardy, 1956; Crisp, 1974).

Although we have not determined how blastulae or gastrulae orient vertically, the observation that they also settle into sucrose gradients with their antero-posterior axis vertical would seem to indicate that either asymmetric distribution of body mass or drag characteristics associated with body shape result in geonegative swimming (see Chia et al., 1984a).

ONTOGENETIC VERTICAL MIGRATION

In the field we found no evidence that plutei undergo an ontogenetic vertical migration (Fig. 1). Thorson (1964) and a number of recent studies (reviewed by Forward, 1976) suggest that larvae of species which inhabit the intertidal as adults remain in surface water throughout larval development, while larvae of species which live subtidally as adults descend into deeper water as they near competency. Thorson's (1964) generalization is in agreement with our data from northeast Pacific waters, where populations of D. excentricus occur intertidally (see Emlet, 1985). However, over most of its species range along the North American west coast, D. excentricus occurs in the shallow subtidal just outside the surf zone (Merrill & Hobson, 1970). Although it is conceivable that differences in larval morphology or behavior exist between animals from the two habitats (see MacGinitie & MacGinitie, 1949), it seems more probable that competent larvae of D. excentricus recruit from surface waters into both intertidal and subtidal habitats (see Ebert, 1983; Chia et al., 1984b).

Ontogenetic migrations of larvae have been widely suggested to occur because advanced-stage larvae of benthic invertebrates become too dense to remain planktonic and thus eventually settle to the bottom (reviewed by Banse, 1964; Thorson, 1964; Forward, 1976). Burke (1978) observed competent larvae of D. excentricus swimming near the bottom of culture dishes and suggested a similar cause. In contrast, our measurements of the specific gravity of larvae indicate that advanced-stage plutei are more buoyant than early plutei (Fig. 5). This decrease in specific gravity in combination with the development of locomotory, ciliated lobes (hypertrophied regions of the ciliary band;

see Strathmann, 1971) on 8-armed plutei probably accounts for the occurrence of competent plutei in surface waters. The decrease in specific gravity of advanced plutei is probably caused by the accumulation of lipid reserves within cells lining the gut (Burke, 1978, 1981) prior to metamorphosis. Lipid reserves may also be responsible for the characteristic yellow color of late plutei (see Highsmith, 1982) and newly-metamorphosed juveniles.

Although the above field and laboratory data are in agreement, our measurements of larval specific gravity are subject to two potential criticisms. Lowndes (1942) pointed out that measurements of specific gravity involving sucrose solutions expose specimens to osmotic stresses that may alter their density. Such alterations could conceivably have affected our results; we nevertheless used a sucrose technique because of its direct simplicity. Second, Paulay et al. (1985) have shown that a variety of larval types, including D. excentricus plutei, can be food-limited in nature. When starved some larval types develop more slowly (reviewed by Day & McEdward, 1984; Paulay et al., 1985); if they also sequester less lipid, field-collected late plutei may have higher specific gravities than well-fed cultured larvae. However, West & Costlow (1980) found that barnacle nauplii grew slower under food-limiation but sequestered about the same amount of lipid during each instar as did well fed nauplii.

Most invertebrate larvae, including echinoplutei (Isono & Yasumasu, 1968), appear to use lipid as their major energetic reserve (reviewed by Crisp, 1976; Holland, 1978; Day & McEdward, 1984). Among those planktotrophic larvae which have been examined (primarily bivalve and barnacle larvae), lipids are accumulated throughout feeding development and then depleted during and immediately following metamorphosis. Lipids are thought to be sequestered instead of other fuels available to zooplankton (e.g., carbohydrate) in part because of its bouyancy (Nevenzel, 1970; Sargent, 1976; Holland, 1978). The specific gravity of marine organisms has not often been measured (but see Gross & Raymont, 1942; Lowndes, 1942; Morris, 1972; Childress & Nygaard, 1974; Spaargaren, 1979), and we are aware of no such measurements upon invertebrate larvae. Nonetheless, those planktotrophic larvae that sequester lipid may not increase in density throughout development as suggested by Thorson (1964). The occurrence of juvenile polychaetes (Banse, 1964) and ophiuroids (Strathmann, 1974) in the plankton and the low

rates of respiration measured for barnacle cyprids (Lucas et al., 1979) might also be explained in this way. Chia (1973) has shown that juvenile D. excentricus ingest sand grains, presumably as an adaptation to increase specific gravity.

Although ontogenetic changes in specific gravity were examined primarily to document differences in density between early and advanced-stage plutei, the most striking increase in density occurred between blastula and pluteus stages. While eggs and embryos are only slightly more dense than seawater (ca. 1.05 g/cc; and see Fox, 1925), early plutei are about 20% more dense (ca. 1.25 g/cc). The consequences of such large density changes are unknown, but it may be advantageous for eggs and embryos to be slightly denser than seawater so that when spawned they are quickly washed into the plankton (see Pechenik, 1979; Pennington, 1985 [Appendix A]), but do not float to the surface where they might be damaged by ultraviolet light (see below). Conversely, although plutei are more dense than pre-pluteus stages and must expend energy to remain in the plankton, the larval skeleton permits growth of arms (see Emlet, 1983) which in turn may increase net energetic intake through lengthening of the food-collecting ciliary band (Strathmann, 1971; McEdward, 1984).

DIEL VERTICAL MIGRATION

In the enclosure and aquarium experiments plutei underwent DVM, descending during daytime and rising slowly towards the surface at night, even though they occurred shallower than 6 m during daytime in the field. In both the enclosure and aquarium, rates of upward movement at night were much slower than downwards sinking during daytime; similar observations are not uncommon (reviewed by Rudjakov, 1970; Chia et al., 1984a). Plutei observed swimming in jars or columns usually swim towards the surface much faster (ca. 1 mm/s) than they ascended in the enclosure or aquarium. While turbulence or other uncontrolled variables in the enclosure and aquarium might account for this discrepancy, it may also be that laboratory measurements of swimming speeds are not representative of rates of larval movement over longer distances.

Laboratory experiments with temperature and vertically-oriented incandescent light did not produce downward movement of plutei. However, experiments with horizontally-directed incandescent light produced horizontal movements of plutei in small

chambers. We have interpreted these movements to be artefacts caused by convection currents. Runnstrom (1918) and Neya (1965; summarized in Yoshida 1966, 1979; Millot, 1975) reported similar results with echinoplutei that may also be artefactual.

Plutei show a striking response to UV light (Fig. 7). We found that plutei descend when exposed to unfiltered sunlight and when irradiated with UV-B at simulated solar intensities. The response is apparently photokinetic because plutei descended towards a UV-B source directed up from below, and is probably under nervous-control because pre-pluteus stages, which do not have an integrated nervous system (see Burke, 1983), did not stop swimming or sink when irradiated. Larvae never responded to UV-A and VIS in our experiments. Exposure to sufficient UV-B to elicit the sinking response was not apparently harmful to plutei, but long-term exposure to simulated natural UV-B intensities (but high daily doses) killed or retarded development of plutei.

Echinoderm larvae have not previously been reported to undergo DVM, and no zooplankter has been demonstrated to do so in response to UV. However, a variety of planktonic invertebrates have been shown to respond to UV, including two echinoid larvae. Fox (1925) reported that plutei of both Diadema setosum and Paracentrotus lividus descended when placed in sunlight in vials. Because the response in P. lividus was more striking in silica rather than glass vials, Fox (1925) concluded that UV was responsible, though he did not suggest that UV might cause DVM in nature. As in the present study, Fox (1925) found that the response is photokinetic and that plutei return to the surface following irradiation. With the exception of two crinoid species (Mortensen, 1921; Dan & Dan, 1941), a holothurian (Young & Chia, 1982), the studies referred to above (Runnstrom, 1918; Neya, 1965) and the misinterpretations in Thorson (1964; also Asterias rubens, see Chadwick, 1914), we are aware of no other reports of photosensitivity among echinoderm larvae. Other zooplankters reported to avoid or respond to UV include ciliates (reviewed by Menzel, 1979), hydromedusae (Ohtsu, 1983a, b), oyster veligers (Aboul-Ela, 1958), Daphnia (Moore, 1912; Baylor & Smith, 1957), barnacle nauplii (Loeb, 1906, 1908, cited in Thorson, 1964), and decapod zoeae (Forward & Cronin, 1979). However, Damkaer & Dey (1982, 1983) studied several crustacean species which apparently do not avoid UV, even in lethal dosages. Some zooplankton can also be killed by visible light (Marshall & Orr, 1955; Hairston, 1976, 1978, 1979, 1980). Visible light and UV-A were

not apparently harmful to D. excentricus plutei.

Some species of adult echinoids also avoid UV, both by covering themselves with debris and by moving into shade (Sharp & Gray, 1962; Lees & Carter, 1972; see Millot, 1975). The "dermal light sense" that has been documented among adult echinoids for visible light (reviewed by Yoshida, 1966, 1979; Millot, 1968, 1975) is probably responsible for the responses to UV as well, though the photoreceptive structures and pigments involved in both adult and larval photosensitivity remain unidentified (Eakin, 1968; Needham, 1974; Millot, 1976; Yoshida, 1979). At least some echinoid plutei apparently do contain pigments that absorb UV (Griffiths, 1965; Ryberg, 1980). Harvey & Lavin (1951) found that the ciliary band, under which pluteus nerves (Burke, 1983) and pigment cells (Ryberg & Lundgren, 1979) lie, strongly absorbs UV. Because adult echinoid nerves are directly photosensitive (Yoshida & Millot, 1959, 1960; reviewed by Millot, 1968, 1975), pluteus nerves may also sense UV directly (see Menzel, 1979; Ohtsu, 1983a, b) and thus control swimming activity. However, Gustafson & Toneby (1970, 1971) suggested that pluteus pigment cells are nervous and produce serotonin which stimulates swimming. Millot (1975) has emphasized that while echinoderm photosensitivity is evolutionarily primitive, it retains adaptive value.

Solar UV between 280 and 315 nm (UV-B) can penetrate to several meters' depth even in coastal waters (Jerlov, 1950, 1970; Calkins, 1975; Zanzeveld, 1975; Smith & Tyler, 1976; Smith & Baker, 1979), and is clearly harmful to aquatic organisms at natural intensities (Ewald, 1912; Klugh, 1930; Seliger & McElroy, 1965; Siebeck, 1978; Karanas et al., 1979; Damkaer et al., 1980, 1981; Damkaer & Dey, 1982, 1983). It is therefore not surprising that shallow-water organisms avoid UV damage. Most commonly, UV-screening pigments have been suggested to protect such animals (Herring, 1965; Needham, 1974; Siebeck, 1978; Jokiel, 1980), though it has not often been determined whether the colored pigments examined actually absorb UV (but see Cheesman et al., 1967; Jokiel & York, 1982). Echinoids from relatively deep water are often lighter in color than conspecific and heterospecific individuals from shallow water (Goodwin & Fox, 1955; Sharp & Gray, 1962; Fox & Hopkins, 1966; Vevers, 1966) and a variety of echinoids darken upon exposure to sunlight (reviewed by Harvey, 1956). McEuen (in press, pers. comm.) has noted that those holothurian eggs which are buoyant and

commonly found floating the water's surface are heavily pigmented (and see Villela, 1956; Cheesman et al., 1967). Conversely, because planktonic animals are often under selective pressure to remain transparent (Hardy, 1956; Chapman, 1976), they might simply move somewhat deeper during daytime to avoid UV. Segal (1970) noted that few invertebrate larvae are found at the water's immediate surface during daytime.

Most precompetent and competent plutei were found less than 6 m deep in the field during daytime, and UV typically penetrates coastal water only a few meters. These observations, in combination with the slow upward migration of plutei observed at night, probably indicate that D. excentricus plutei migrate, at most, one or a few meters during each 24 h. If so, the DVM probably does not function to regulate rates of metabolism, feeding and encounters with predators as suggested for zooplankters which undertake extensive DVM's (reviewed by Longhurst, 1976). Instead, the opposing geonegative and photonegative behaviors of plutei probably serve to keep them in surface waters, but below harmful levels of UV irradiation.

Table I. Survival of 50, 4-armed plutei in each of several shallow bowls (ca. c cm deep) 3 days following either: (1) 20 min irradiation with "full intensity" UV-B (plus UV-A and VIS) from above; or (2) no irradiation. After treatment the bowls were placed in an 12 degree C water bath under ambient laboratory lighting.

	IRRADIATED PLUTEI (4 bowls)	CONTROL PLUTEI (2 bowls)
MEAN	49	49
STANDARD ERROR	0.91	0

Figure B-1. Mean vertical distributions of pre-competent (top) and competent (middle) plutei of Dendraster excentricus in in Eastsound, Washington on 6 dates during the spring and summer of 1983. "Percent occurrence" refers to the percent of plutei of a given stage captured at a given depth; all values are standardized to volume of water sampled. The ">>10 m" sample was taken near the bottom (ca. 20 m) 10-15 m deep. Numerals within or alongside pyramids indicate number of replicate samples (in which some larvae were found at any depth) taken at that depth. Temperature and salinity profiles taken at several stations on Aug. 22, 1983, are also given at bottom.

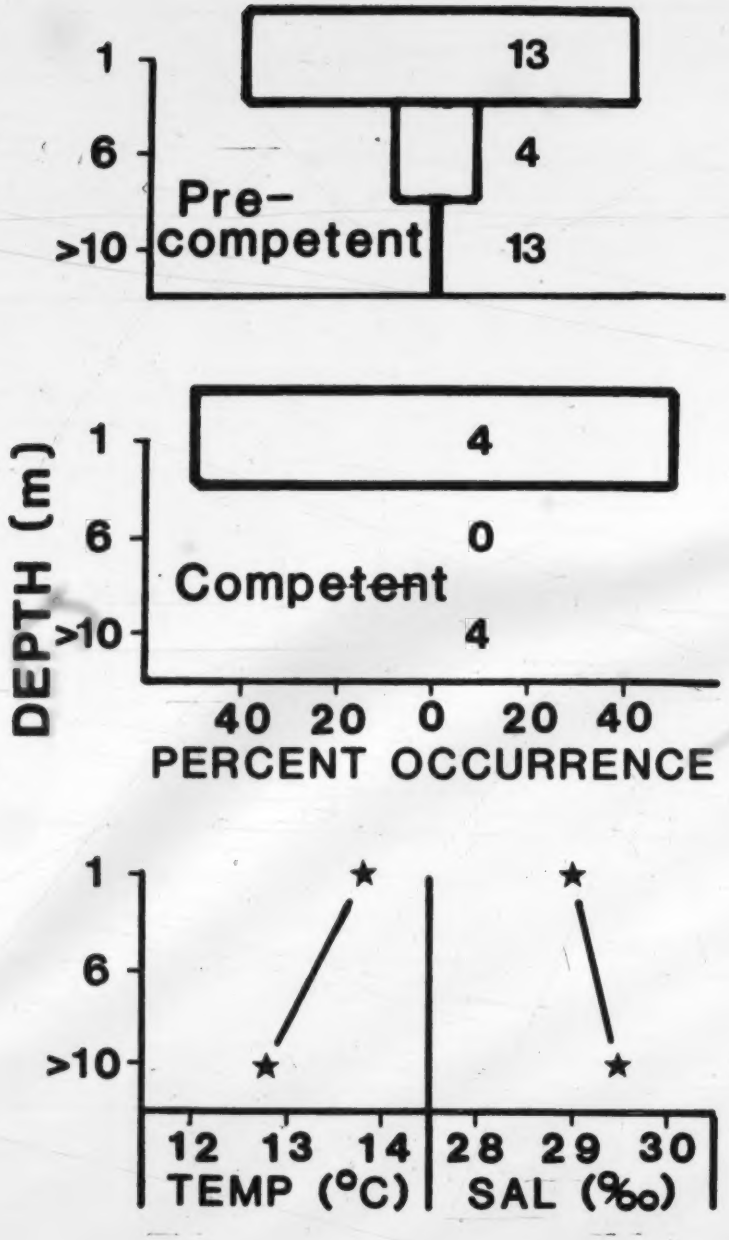

1
6
>10
Pre-
competent
13
4
13
DEPTH (m)
1
6
>10
Competent
4
0
4
40 20 0 20 40
PERCENT OCCURRENCE
1
6
>10
12 13 14
TEMP (°C)
28 29 30
SAL (‰)

Figure B-2. Vertical distribution of early 4-armed, advanced 4-armed, 6-armed and 8-armed plutei in a 2500 l floating enclosure during each of 5 sampling sessions over 24 h. "Percent occurrence" refers to the percent of plutei of a given stage captured during that sampling session at a given depth. A mean of 1009 larvae were sampled per pyramid (stage x sampling session); the minimum number of plutei of any stage captured during any sampling session was 75. Light intensity and temperature at each depth during each sampling session are plotted at the bottom of the figure. Salinity did not vary with depth within the enclosure.

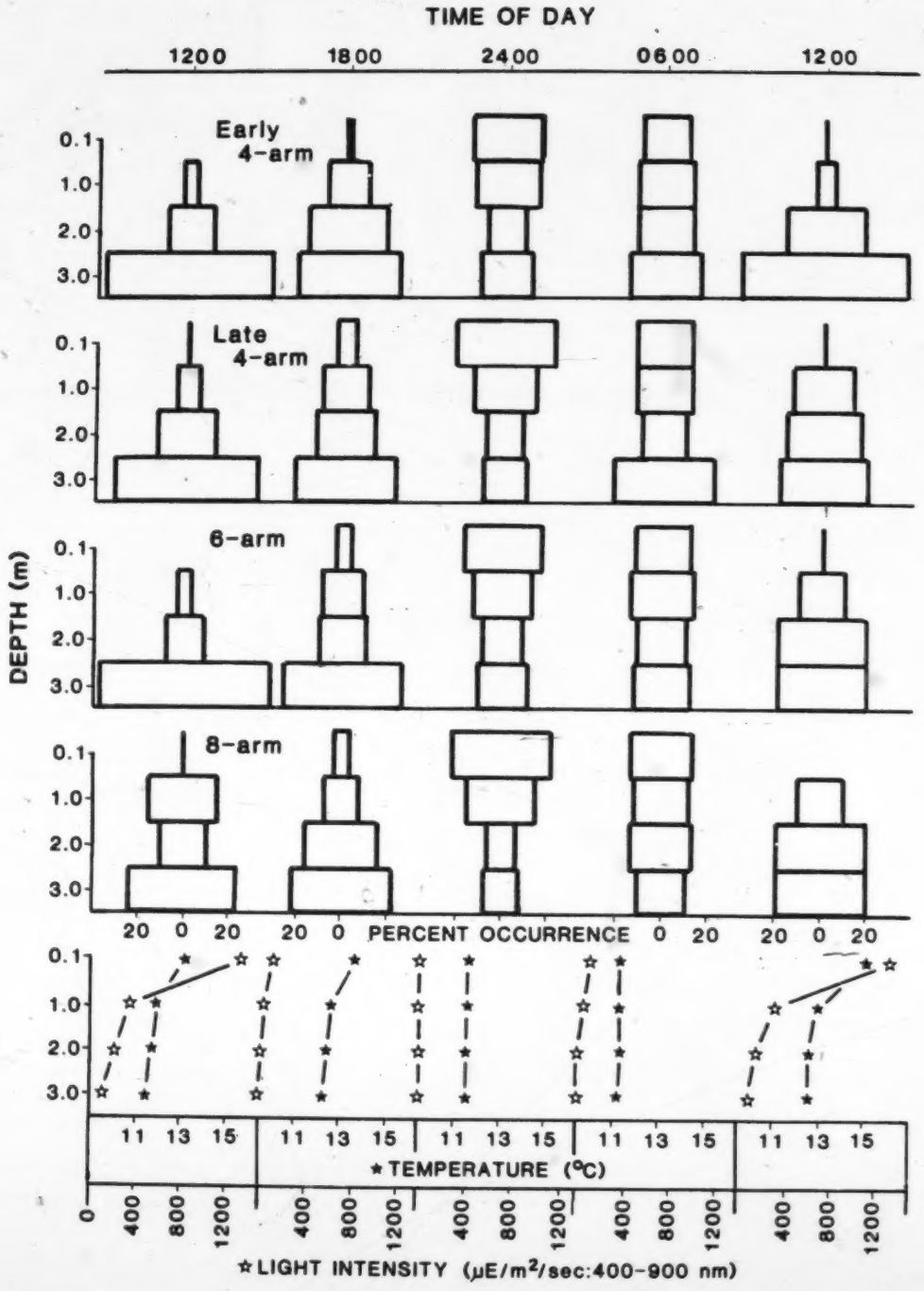

TIME OF DAY
1200
1800
2400
0600
1200
Early 4-arm
Late 4-arm
6-arm
8-arm
DEPTH (m)
0.1
1.0
2.0
3.0
20 0 20 20 0 PERCENT OCCURRENCE 0 20 20 0 20
11 13 15
TEMPERATURE (°C)
0 400 800 1200
LIGHT INTENSITY (μE/m²/sec:400-900 nm)

Figure B-3. Vertical distribution of 4-armed plutei in a 1500 l outdoor aquarium during each of 3 sampling sessions over 24 h. "Percent occurrence" refers to the percent of plutei captured during that sampling session at a given depth. A mean of 6340 larvae were sampled per pyramid; the minimum number of plutei captured during any sampling session was 3890. About 12 h prior to the final sampling session, a nearly opaque plastic cover was placed over the aquarium so that larvae remained in near-darkness the following day. Light intensity and temperature at each depth during each sampling session are plotted at the bottom of the figure. Salinity did not vary with depth within the aquarium.

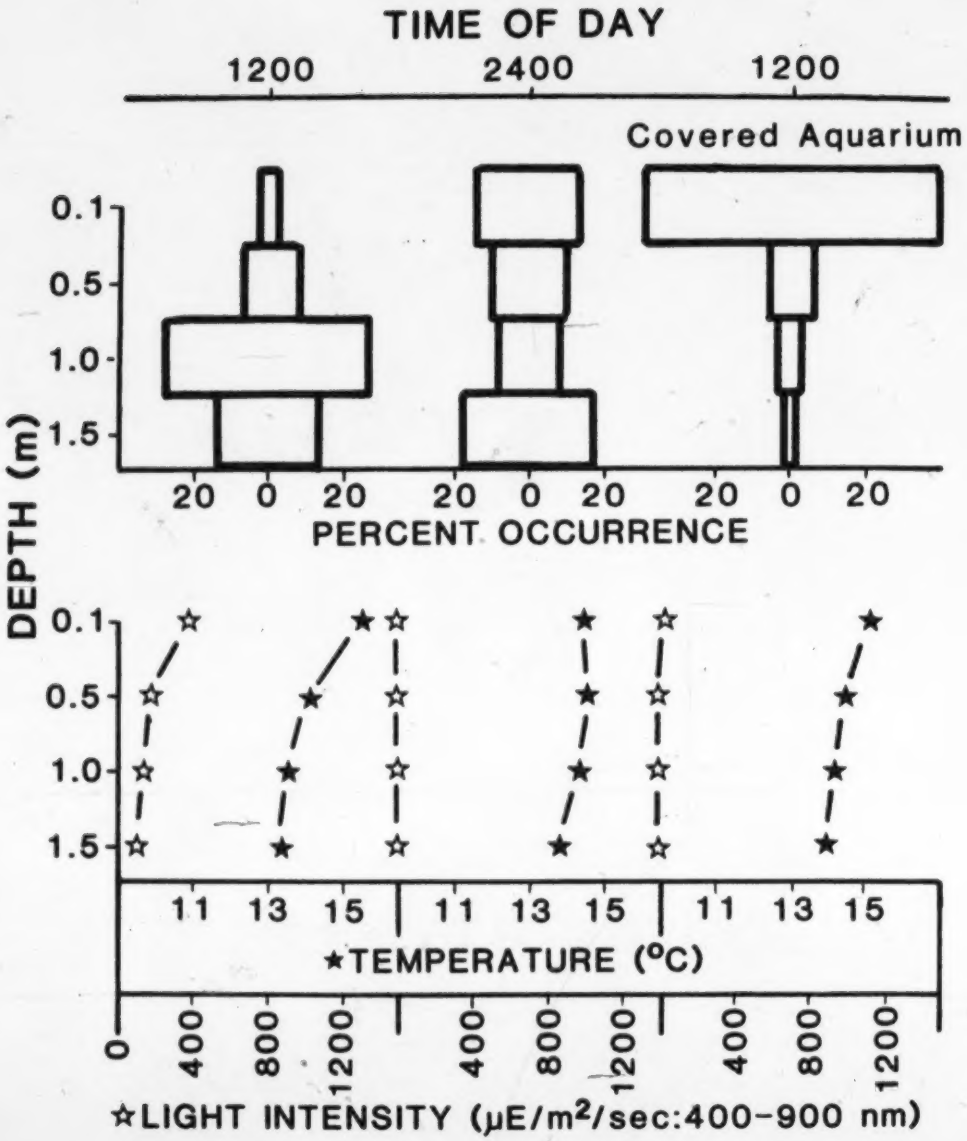

TIME OF DAY
1200
2400
1200
Covered Aquarium
DEPTH (m)
0.1
0.5
1.0
1.5
20 0 20 20 0 20 20 0 20
PERCENT OCCURRENCE
11 13 15 11 13 15 11 13 15
★TEMPERATURE (°C)
0 400 800 1200 400 800 1200 400 800 1200
☆LIGHT INTENSITY (μE/m²/sec:400-900 nm)

Figure B-4. Photograph taken from above, onto dead plutei floating on a discontinuity between seawater and a sucrose:distilled water solution slightly denser than the plutei. All pluteus stages oriented posterior downwards and arms upwards.

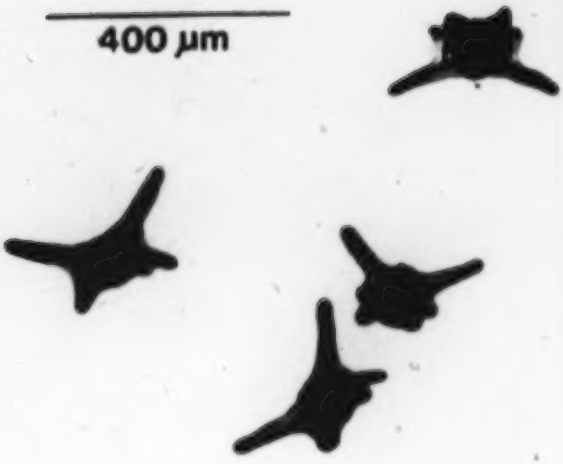

400 µm

Figure B-5. Density of eggs, embryos, larval stages and 20 h old juveniles of D. excentricus. The vertical bars are not error bars, but represent the minimum difference in density between sucrose solutions upon which 50-100 individuals of each stage floated, or through which they sank at 18° C.

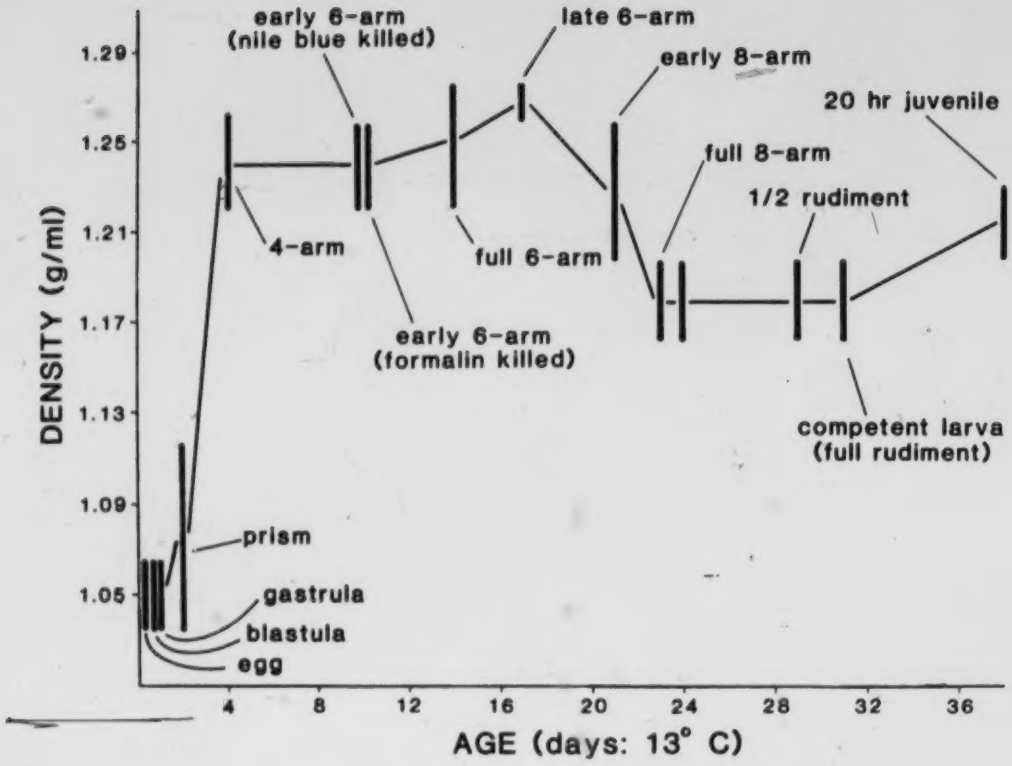

early 6-arm
(nile blue killed)
late 6-arm
early 8-arm
20 hr juvenile
full 8-arm
1/2 rudiment
4-arm
full 6-arm
early 6-arm
(formalin killed)
competent larva
(full rudiment)
prism
gastrula
blastula
egg
DENSITY (g/ml)
1.29
1.25
1.21
1.17
1.13
1.09
1.05
4
8
12
16
20
24
28
32
36
AGE (days: 13° C)

Figure B-6. The effects of a horizontal beam of incandescent light on distribution of plutei within small chambers: (A) Schematic drawing of an apparent aggregation of plutei near the middle of the chamber after 5 min of illumination. The small v's represent individual plutei. Such aggregations moved away from the light source with increasing periods of illumination; (B) Movement of dye in convection currents created by the light's heat in the chamber. Such convection cells increased in length with increasing periods of illumination; (C) Schematic drawing of the interaction between upswimming by plutei and the convection currents that created the apparent aggregations. The plutei uniformly swam up and were thus carried along in either upwards or horizontal currents. However, plutei swam against downwards currents and thus were concentrated in them, producing the aggregations.

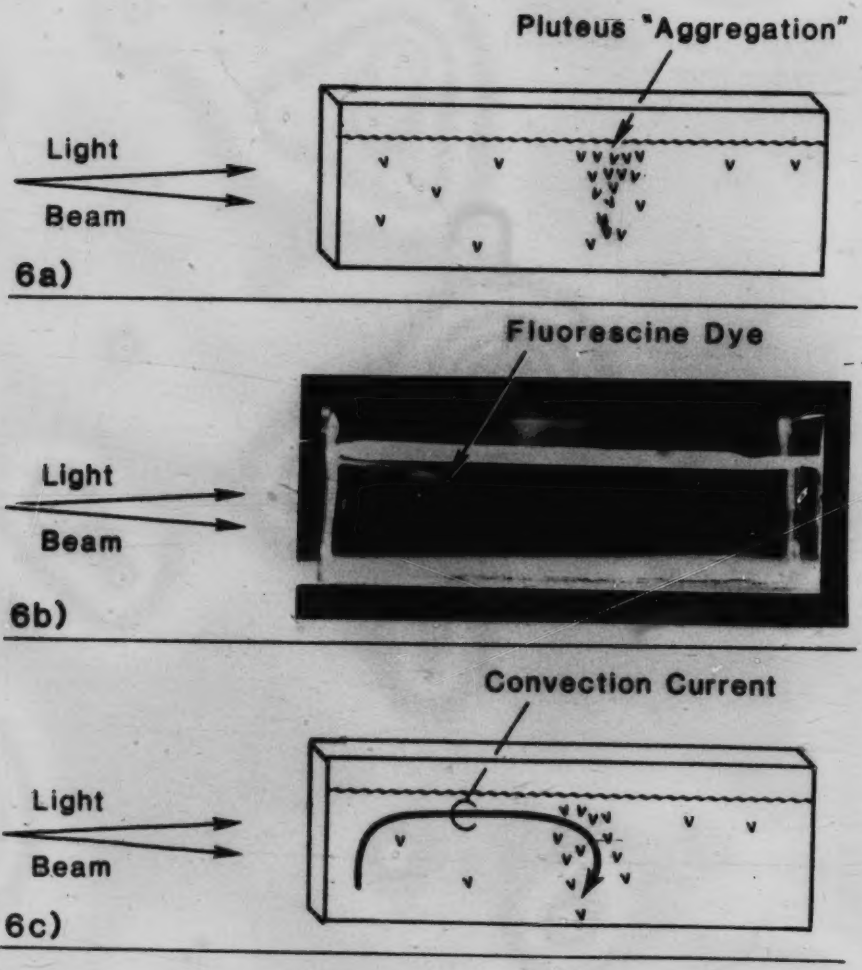

Pluteus "Aggregation"
Light
Beam
6a)
Fluorescine Dye
Light
Beam
6b)
Convection Current
Light
Beam
6c)

Figure B-7. Scintillation vials containing seawater and about 100 4-armed plutei (arrows): (A) swimming near the water surface prior to irradiation; (B) on the bottom of a vial following 20 min irradiation from above with full intensity UV-B (see Methods).

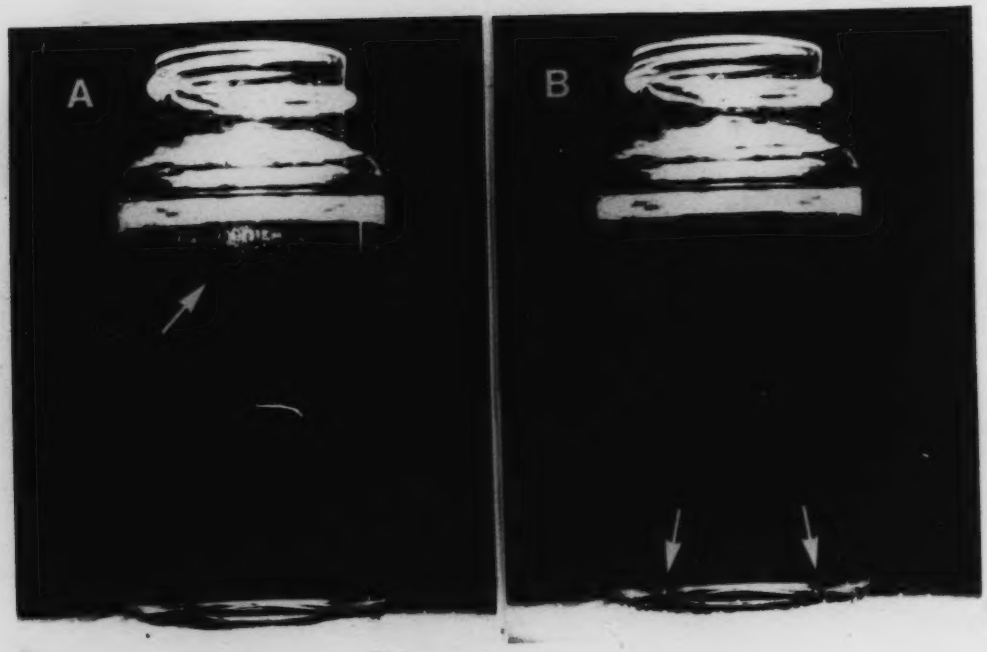

A
B

Figure B-8. Mean vertical distribution (± 1 standard error) of 10, 4-armed plutei in each of 6 replicate 3 ml spectrophotometer cuvettes (1) before irradiation, (2) after 20 min irradiation from above with full intensity UV-B (plus UV-A and VIS), (3) after 5 min additional irradiation following a gentle rocking or tapping of the cuvettes, and (4) an hour after the lights were turned off. Larvae were visually scored as being either within 1 mm of the water's surface, within the water column, or within 1 mm of the bottom.

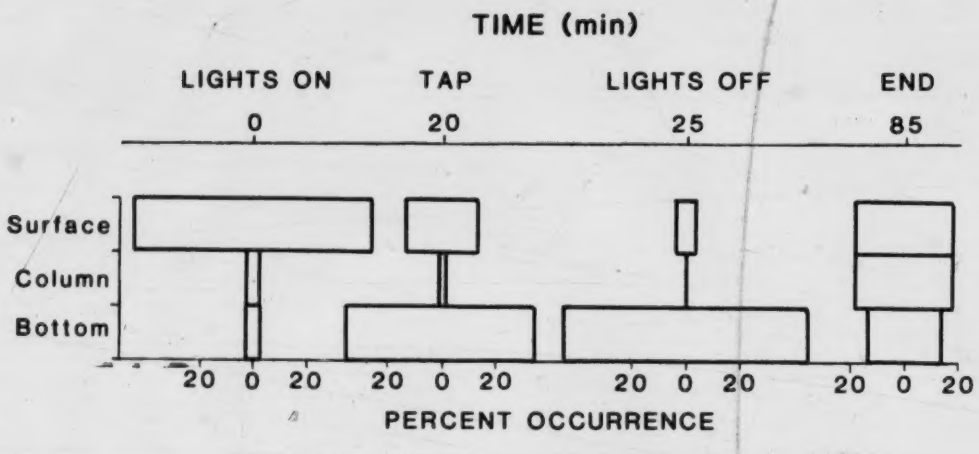

TIME (min)
LIGHTS ON
TAP
LIGHTS OFF
END
0
20
25
85
Surface
Column
Bottom
20 0 20
20 0 20
20 0 20
20 0 20
PERCENT OCCURRENCE

Figure B-9. Mean survival (± 1 standard error) of 4-armed plutei when confined in shallow bowls (ca. 3 cm deep) and subjected to 8 h daily exposure to either: (1) ambient laboratory (indirect fluorescent and window) lighting only; (2) UV-A (and VIS); (3) half intensity UV-B (plus UV-A and VIS); (4) full intensity UV-B (plus UV-A and VIS); (5) double intensity UV-B (plus UV-A and VIS). Larvae in at least 2 bowls from each treatment were fixed and counted every second day.

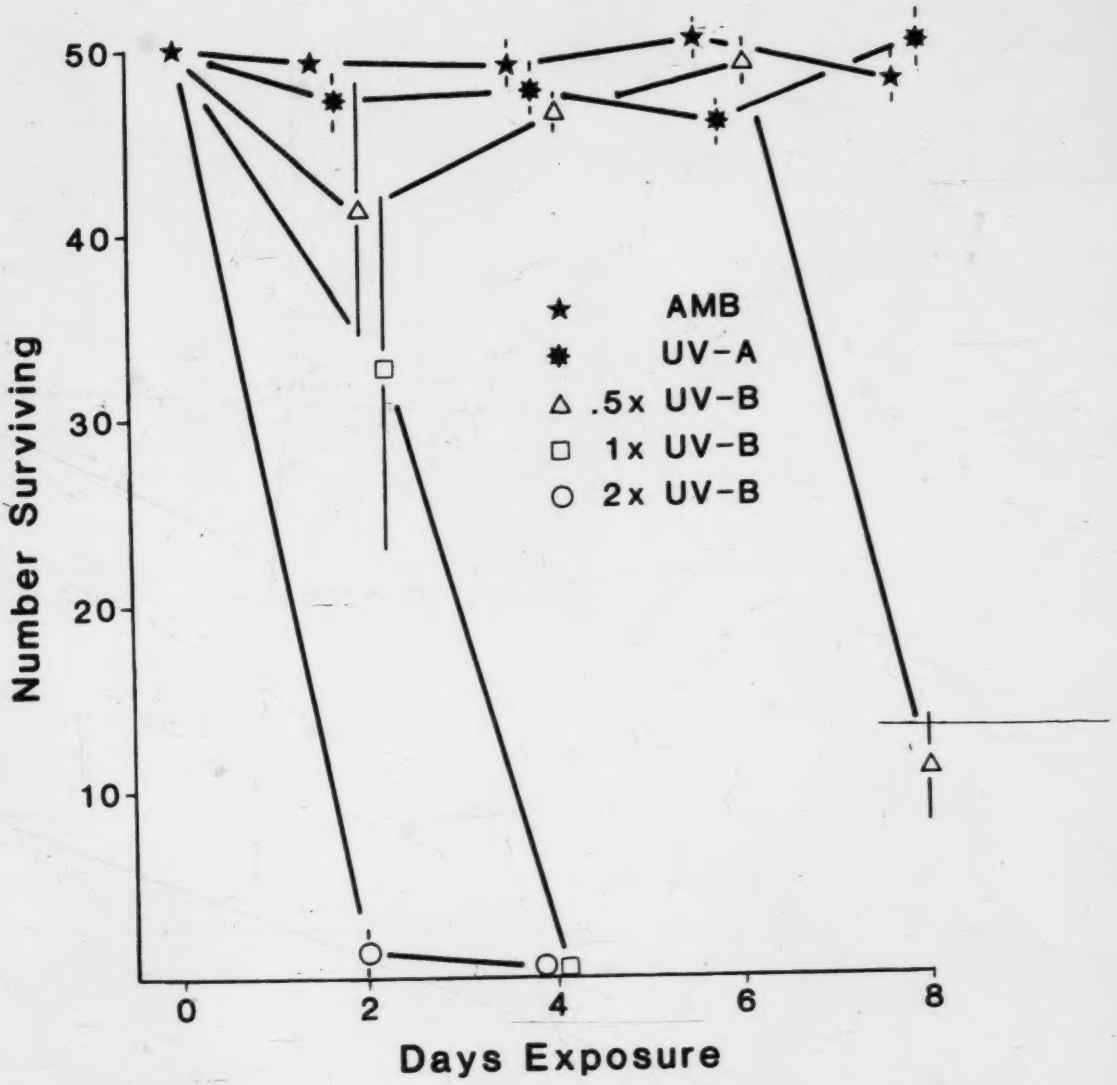
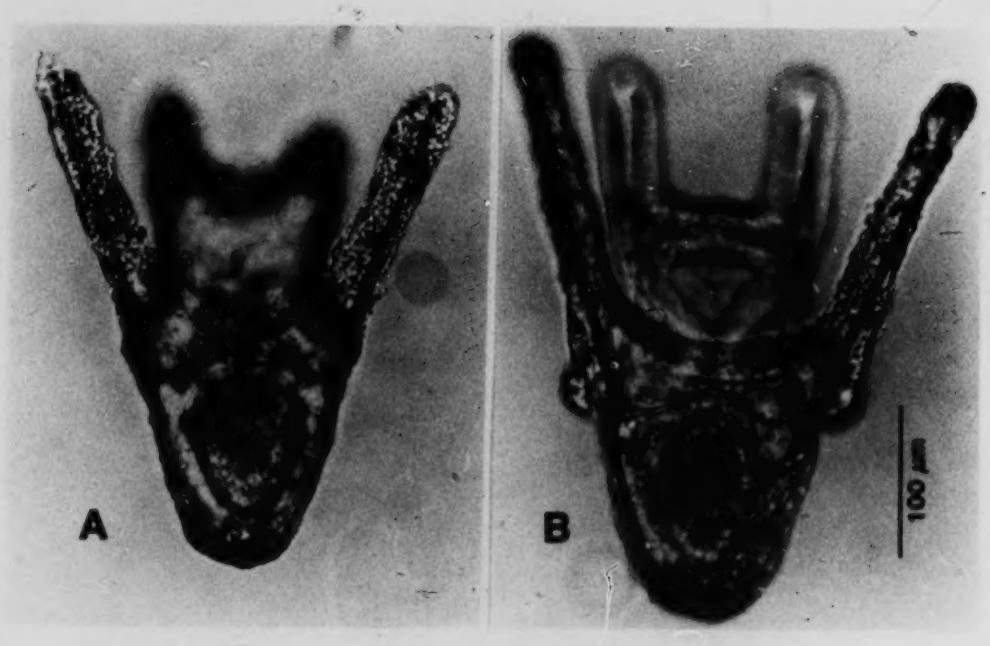

50
40
30
20
10
Number Surviving
0
2
4
6
8
Days Exposure
AMB
UV-A
.5x UV-B
1x UV-B
2x UV-B

Figure B-10. Four-armed plutei confined in shallow bowls (ca. 3 cm deep) and subjected for 4 days to 8 h daily exposure to either (A) half intensity UV-B radiation (plus UV-A and VIS) or (B) ambient laboratory lighting only. Irradiated plutei swam slowly at the bottom of dishes, appeared blotchy, and had not grown since the beginning of the experiment. Photographs are to same scale.


A
B
100 µm

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April 3, 1986

Mr. John Timothy Pennington
Department of Zoology
University of Alberta
Edmonton, Alberta
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Dear Tim,

You have my permission to include in your dissertation as an appendix our collaboration entitled: "Ontogenetic and diel vertical migration of a planktonic echinoid larva, Dendraster excentricus (Eschscholtz): occurrence, causes, and probable consequences".

It has been a pleasure working with you.

Sincerely,

Richard B. Emlet

Richard B. Emlet

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Mr. Tim Pennington
Graduate Student
Department of Zoology
University of Alberta
EDMONTON, Alberta

April 25, 1986

Dear Tim:

Thank you for your letter of January 13, 1986.

I am happy to grant you permission to use our collaborations in your thesis. The first is entitled "Stage-specific predation upon embryos and larvae of the pacific sand dollar, Dendraster excentricus, by eleven species of common zooplanktonic predators." The second is entitled "Morphological and behavioral defenses of trochophore larvae of Sabellaria cementarium against four planktonic predators." The third is entitled "Gastropod torsion: a test of Garstang's hypothesis."

Good luck to you.

Yours sincerely,

F.S. Chia--Dean
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FSC:mac

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28 April1986

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Dear Tim:

Thank you for bringing the topic of jointly-authored publications to my attention. You have my full consent to use our collaborative article in the third chapter of your thesis. The article is entitled "Stage-specific predation upon embryos and larvae of the pacific sand dollar, Dendraster excentricus, by eleven species of common zooplanktonic predators."

I hope we will have opportunity to collaborate again.

Best Regards,

Mr. Steven S. Rumrill

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CHARLES B. METZ
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BIOLOGICAL BULLETIN

March 5, 1986

Mr. J. Timothy Pennington
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Dear Mr. Pennington:

We are happy to grant you permission for use of the material from The Biological Bulletin, as specified in your letter of 19 February 1986 for your forthcoming publication. This permission is subject to the usual acknowledgments being made to this journal as the place of original publication, and applies to all languages and for countries throughout the world. We prefer that you also obtain the permission of the author or authors, if it is feasible for you to do so.

Yours sincerely,

Charles B. Metz

Charles B. Metz
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